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# Twenty years of temperate montane forest progression in the oldest Polish national park

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**Abstract** The historical fragmentation of forest ecosystems led to a significant spatial reduction in natural forest biomes. After centuries of exploitation for various purposes, the fragments remaining as national parks have been systematically monitored. This provides a wide range of field data and allows an in-depth understanding of processes responsible for short- and long-term forest dynamics. The existing monitoring systems should be considered unique and worth maintaining because they spanned before the era of remote sensing data acquisition in sufficient spatial and temporal resolution. We explored tree monitoring data from the oldest national park in Poland – Pieniny National Park (PNP) in the Western Carpathians, established in 1932. We assessed stand aboveground increment, recruitment, and mortality for 44 monitoring plots with field observations obtained in 1987, 1998, and 2009. Using a linear mixed-effects model, we assessed differences in stand biomass among sampling years and determined the drivers of biomass dynamics. For relative values of increment, recruitment, and mortality, we developed generalized linear mixed-effects models with a Beta distribution of the dependent variable. We found that stand composition was only slightly affected across 22 years. The mean aboveground biomass increased evenly and significantly (from 168 to 237 Mg/ha). Stand dynamics were mostly affected by stand structure characteristics, especially basal area (BA) and density, while other factors (geomorphometric and climatic characteristics) modified these relationships. The importance of climatic and geomorphometric factors shows local responses of stand dynamics, which can be utilized for fine-scale sites. We found twice higher relative increments in SW than in NE exposition, which can be related to higher insolation (sunlight and temperature) on SW-exposed hillslopes. The aboveground tree biomass change caused by mortality was partly controlled by several variables, among which the most important was BA. With increasing BA, mortality increased and was also slightly related to steeper slopes. Species-specific trends were dominated by species proportion. *Fagus sylvatica* had higher relative increment and mortality in plots with its dominance, while *Abies alba* absolute increment decreased. Studying the mountain forest dynamics is crucial for biodiversity, soil and groundwater protection, and tourism. Ground measurements are an accurate way to estimate biomass.

**Keywords:** *Abies alba*, aboveground biomass, *Fagus sylvatica*, increment, monitoring, mortality, recruitment

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## Introduction

Natural forests are a subject of constant change overlapped by periodic pulses related to disturbances (Seidl et al. 2017, McDowell et al. 2020, Romeiro et al. 2022). At the same time, forests act as a sensitive buffer layer (envelope) formed over the Earth's surface, where various environmental and anthropogenic influences accumulate and contribute to a constant flow of mass and energy. Abiotic and biotic disturbances prevailed until a specific time in the Earth's history. However, along with a fast expansion of human settlement and activity, the situation shifted to conditions where man-induced stress factors dominated (Nascimento et al. 2024). The most extreme cases include forest dieback due to air pollution at the German-Czechia-Polish border zone in the 1980s/1990s (Mazurski 1986), defoliation of tropical forests caused by chemical compounds used by the American Army during the war in Vietnam in 1960s (Orians & Pheiffer 1970), forest damage due to military actions in Europe during the 2nd World War (Waga et al. 2022), and during ongoing Russian War in Ukraine (Matsala et al. 2024). From the perspective of the present knowledge on the rate of past changes, certain sudden events (e.g., Bond cold climate events and subsequent warming during the Holocene) were an integral part of the Earth system, impacting forest ecosystems in multiple ways (Bond et al. 2001). However, it was also acknowledged that along with fluctuating and evolving climate, human activity, especially widespread deforestation during the Late Holocene time, caused enormous acceleration of changes in forest growth conditions (i.e., forest area, structure, health conditions, species distribution, etc.) and land cover properties, i.e., unprecedented increase in the soil erosion rate after deforestation (Anselmetti et al. 2007). Today, human activity and its impact on forests is evident and generally evaluated as negative (Hanewinkel et al. 2013; Hansen et al. 2013). However, forests play multiple functions, benefiting both societies and the environment. Hence, the forest condition and quantitative evaluation of their aboveground biomass should be the critical subject of concern and research. Part of the world's forests is protected under national parks and nature reserve entities. The issue of forest protection and the problem of its exploitation is global and deeply discussed, especially when the subject of the investigation is the Amazonian rainforest under excessive deforestation for agricultural purposes (Carvalho et al. 2017), Canadian forests under wildfire (Coogan et al. 2019), or the Białowieża Primeval Forest suffering from over-intensified exploitation for economic purposes (Latałowa et al. 2015). As European forests entered the 21st century, it was also argued that the effects of global environmental changes related to man-induced climate warming would be more severe in mountain regions (Loarie et al. 2009; Steinbauer et al. 2018), affecting montane forests, which are essential for biodiversity, groundwater resources, and soil protection, and for the economy.

European forests can be threatened by land-use changes, air pollution, bark beetle (*Ips typographus*) outbreaks, windstorms, wildfires, drought, and geomorphic agents – landsliding, snow avalanches, debris flows, and soil erosion (Schelhaas et al. 2003; Seidl et al. 2014, 2017; Senf et al. 2018, Senf and Seidl 2021; Šamonil et al. 2021; Patacca et al. 2023). These factors cause different-scale fluctuations and changes in the aboveground biomass of natural forests. In periods of average growth, the factors necessary for long-term forest development include 1) the density-dependent self-thinning mechanism, 2) the culmination of growth, and 3) a higher growth rate of younger stands (Sun et al. 2018). Recruitment is a light-regulated process strongly controlled by forest canopy disturbances (Bao et al. 2024). The climate is strongly correlated with the elevation and the relative height of local and regional landforms. Hence, macro- and microclimate have a significant impact on the growth dynamics in the mountain forests (Hlásny et al. 2011; Cazzolla Gatti et al. 2019; Dyderski and Pawlik 2020; Latterini et al. 2024; Idoate-Lacasia et al. 2024). The geomorphological factors affect global and local trends in forest development (Birkeland et al. 2003; Rice et al. 2012). These include, among others, elevation, aspect, slope, and potential soil moisture that can be evaluated by the topographic wetness index (TWI) (Stage 1976).

In the present study, we explore the 22-year monitoring data on forest ecosystems forming the vegetation belt in unmanaged forests in the oldest national park in Poland, the Pieniny National Park, established in 1932. We aimed to assess the natural dynamics and drivers of stand aboveground biomass over 22 years in unmanaged *A. alba*-*F. sylvatica* forests. We hypothesized that (1) due to changing climate favoring more beech and fir and decreasing habitat suitability for spruce (Dyderski et al. 2025), we expected shifts in stand species composition in this direction, similarly to other national parks in Poland (e.g. Dyderski et al. 2023), (2) we expect that both increasing basal area and density will be correlated with an increase in recruitment (indicating stand maturation and effective regeneration), increment, and mortality, and (3) geomorphometric and climatic characteristics modified the relationship between stand structural characteristics and biomass dynamics, as increased temperatures and higher sun exposition can increase growth rate of trees, while steeper slopes can decrease it and increase susceptibility to disturbances.

# Materials and Methods

## Study area

The study area was the Pieniny National Park (PNP), located in the central part of the Pieniny Klippen Belt. The Pieniny Mountains (49° 22-27′ N, 20° 18-36′ E) with their highest culmination Mt Wysoka (1050 m a.s.l.), are surrounded by higher mountain massifs and from the west by the tectonic trough of the Orawsko-Nowotarska Valley. The Pieniny are composed of many different rock layers dominated by limestone. Other rocky layers include slates, marls, radiolarites, and sandstones (Birkenmajer 2017). The underlying calcareous base creates a bedrock for rendzina and pararendzina soils (Kabała 2018), characterized by high carbonate content, as well as sandstones and shales, which are parent materials for brown soils (Niemyska-Łukaszuk et al. 2004).

The Pieniny Mountains differ from neighboring ranges and are characterized by a mild climate. They are located in the "rain shadow" of the Tatra Mountains and

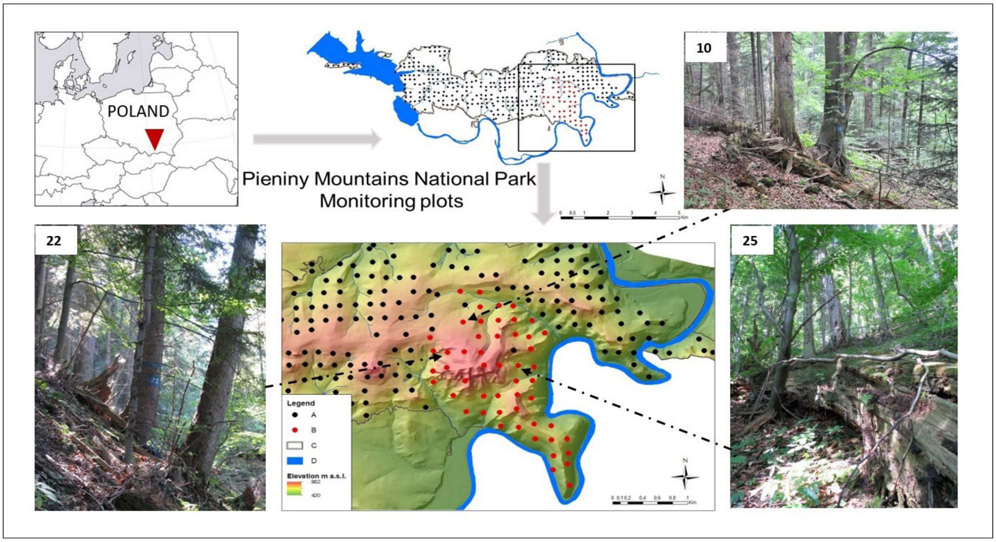

**Figure 1** Study area with localities of permanent monitoring plots. Selected examples of plots 10, 22, and 25. Legend: A - permanent study plots, B - selected plots with the most extended datasets (marked red), C - border of Pieniny National Park, D: rivers, streams, and reservoirs. Photos: J. Bodziarczyk.

are characterized by a relatively low average amount of rainfall. The precipitation depends on the elevation, ranging from 690 to 850 mm, but the total precipitation during the growing season varies from 440 to 750 mm (IMWM - NRI 2023). The number of days with snow cover ranges from 98 (in the valleys) to 140 (around summits). The mean annual temperature ranges from 6.3°C to 3.9°C. The coldest months are January and February, with mean lowest air temperatures from -2.7°C to -1.0°C. However, the absolute minimum can reach from -30.2°C to -36.3°C. The warmest months are July and August, with average temperatures from 13.7°C to 16.4°C. The highest air temperature has been recorded in concave relief forms, ranging from 32.8°C to 34.7°C (Perzanowska 2004).

The Pieniny National Park (PNP) was established in 1932 as the first national park in Poland. PNP and its Slovak counterpart were Europe's first international nature parks (Tyszkiewicz 1992; Michalik 2005). PNP is the second smallest national park in Poland, covering an area of 2346 ha, of which 72% is covered by forests, including 35% private woods. The area of the Park extends from 420 to 982 meters elevation (Figure 1). Many natural communities coexist in the Pieniny Mountains, e.g., afforested areas, as well as rocky and scree clusters. Over 31% of the area is under strict protection, 23% under partial protection, and the remaining part is administered as landscape-protected land. The association *Dentario-glandulose–Fagetum* occupies most of the Pieniny National Park (approx. 39.5%), while xerothermic Beech and Fir stands (*Carici albae-Fagetum*) occupy 25.8%. The most of them are mixed, heterogeneous stands (Figure 2). Silver fir is the most abundant species in the Pieniny forest (Dziewolski 1980; Bodziarczyk et al. 2016), whose share is almost 64%. Apart from fir, only the share of beech is significant and can reach up to 16% while spruce consists 7%. Other tree species are barely noticeable; however, they are an essential part of the biodiversity of the area. Forests of the Pieniny Mountains were a subject of intense exploitation by clear-cuts for agricultural, mining, and building construction purposes until the area was protected as a national park in 1932. However, just a fraction of the current national park zone was under strict protection at this time. According to the archive data presented on the map produced by the Second military survey of the Habsburg Empire (1819-1869), the first significant deforestation happened before 1819 (www.mapire.eu; Timár et al. 2006). In addition, archive data and photographs from the period just before the national park establishment indicate far-reaching deforestation and subsequent forest regeneration, which took several decades (Figure 2).

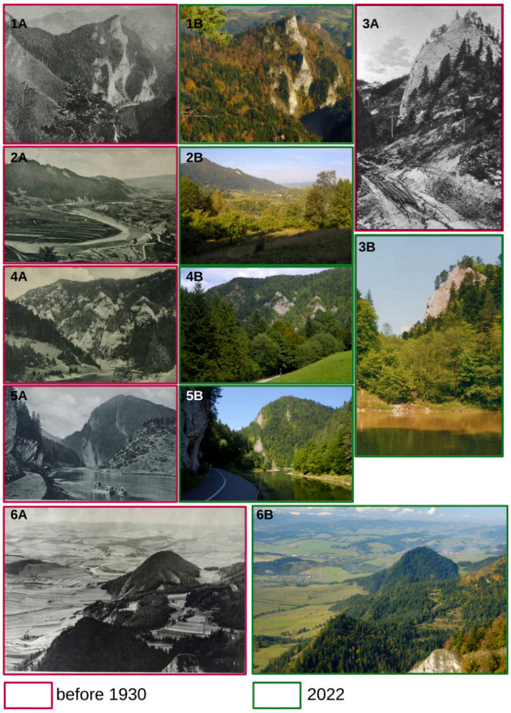

**Figure 2** A historical context of deforestation and forest regeneration in selected parts of the Pieniny National Park. Photos 1A-6A: PNP archive. Photos 1B, 2B, and 4B-6B: Maciej Szajowski (reproduced with the author's permission). Photo 3B: Jan Bodziarczyk.

## Monitoring network design and field data collection

The data were collected in permanent study plots, systematically distributed in *200 × 200 m nodes* of a square *grid* (Figure 1). Initially, the plots were distributed in the areas established as protected the earliest, but over time, they were extended to the entire area of the PNP (Dziewolski 1980). Comprehensive studies of changes in forest vegetation were initiated after PNP establishment, based on a regular network of permanent research plots (Dziewolski 1992; Różański et al. 1994; Bodziarczyk et al. 2016). In this study we focused on the oldest part of the park, located in the zone of strict protection, with no management since 1932. Each study plot consists of two concentric circles with an area of 0.05 ha and 0.01 ha. During the survey, each tree with a diameter at breast height (DBH) ≥7 cm was measured (DBH), and positioned using a polar coordinates system, to repeat tree-level measurements. Moreover, the height of all trees within the smaller subplot was measured. Field assessments were conducted in an 11-year cycle: in 1987, 1998, and 2009.

## Data selection and pre-processing

Due to a lack of measurements in all three dates and the complete set of plots, we excluded plots with incomplete data or significant relocation bias, resulting in an unreliable estimate of mortality and recruitment. Thus, we used measurements from 44 study plots on three dates for data analyses. For each tree we used DBH and height measurements to estimate aboveground biomass using species-specific allometric models, (Alberti et al. 2005; Forrester et al. 2017; Jagodziński et al. 2018, 2019, 2020). The diameter-height relationship was estimated using Naslund's formula. (Table S1). In these models, we used DBH as a predictor, accounting for plot-specific dependency as a random effect, except *Picea abies*, where the model with random effects did not reach a convergence due to the small number of plots (n=9) with this species.

After calculating the total stand aboveground biomass for each study plot and year, we assigned each tree biomass to one of three categories: mortality, recruitment, and increment, following a procedure described by Dyderski et al. (2023). Trees recorded for the last time in a particular year were assigned as mortality, as these trees most probably died before the next census. Similarly, we classified trees recorded for the first time in a particular time as recruitment, assuming that they reached the recording DBH threshold between inventories (Figure 3). For each plot we also calculated stand density (number of trees per area) and basal area (area of trees at 1.3 m height per area; Table 1) as metrics describing tree quantity and the dynamic phase of stand development.

We used data from the CHELSA dataset to assess climatic conditions in 1 km spatial resolution and one-month temporal resolution (Karger et al. 2017; Karger and Zimmermann 2018). We calculated the mean annual temperature, mean winter temperature (January-March), mean summer temperature (June-August), mean annual precipitation, and mean summer precipitation for the last ten years since each inventory (Table 1). We also acquired an open-source 5 m spatial resolution Digital Terrain Model (DTM) (GUGiK 2022). We calculated several geomorphometric terrain characteristics: aspect, slope, Topographic Wetness Index (TWI), Terrain Ruggedness Index (TRI), Topographic Position Index (TPI), Slope Length and Steepness factor (LS factor), Valley Depth, and Relative Slope Position. For computation, we used the *terra* R package (Hijmans 2023) and SAGA GIS 7.8.2 (Conrad et al. 2015). To obtain more interpretable values of aspect, measured as azimuth in degrees, we used Beers's transformation (Beers et al. 1966), based on the cosine of aspect. This transformation returns the lowest values (0) in the north-eastern aspect and the highest (2) for the south-western, reflecting an increase in both the impact of high insolation and high afternoon temperatures(Idoate-Lacasia et al. 2024).

The Topographic Wetness Index reflects the influence of topography on the local hydrological conditions (Sørensen and Seibert

2007). The Terrain Ruggedness Index represents the variability of the local elevation differences (Riley et al. 1999). Topographic Position Index values result from comparing the given cell elevation and the mean elevation within the specified surroundings around this cell (Guisan et al. 1999). LS factor quantifies the impact of hillside length and hillside steepness for each raster cell and indicates the potential soil erosion (Desmet and Govers 1996). The Valley Depth and Relative Slope Position parameters are related to the location of a given raster cell within the prominent terrain landforms (such as valley, slope, and ridge) (Böhner and Selige 2006).

### Data analysis

All analyses were conducted using R software (R Core Team 2023). Mean values are followed by the standard error. We compared stand species composition using Principal Components Analysis (PCA), implemented in the ***vegan*** package (Oksanen et al. 2018). For PCA, we treated each study plot in each year as an observation and the proportion of each tree species in the stand aboveground biomass as a variable. Before PCA, we log-transformed all variables. The first axis of PCA (PC1) served as a predictor of stand biomass dynamics, as PC1 represents the transition from *A. alba*-dominated forests (low values of PC1) towards *F. sylvatica*-dominated forests (high values of PC1).

We assessed differences in stand biomass among sampling years using a linear mixed-effects model (LMM), using sampling year as a fixed effect and plot identifier as a random intercept, to assess pairwise differences for particular plots. For absolute values of increment, mortality, and recruitment, we developed LMMs with all hypothesized factors (Table 1) as independent variables and two random intercepts: study year and plot identifier. For relative values of increment, mortality, and recruitment (related to standing biomass), we assumed the Beta distribution of the dependent variable, and we developed generalized linear mixed-effects models (GLMMs). In these models, we also included all hypothesized factors (Table 1) as independent variables and two random intercepts: study year and plot identifier. We selected variables based on Akaike's Information Criterion for each dependent variable, corrected for small sample size (AICc). For AICc-based selection, we used the dredge() function from the

**Table 1** List of predictors of stand dynamics, their distributions, and variance inflation factors (VIF) for the whole set of predictors and after excluding collinear variables (VIF*).

| Variable | Min | Q1 | Median | Mean | SE | Q3 | Max | VIF | VIF* |
|---|---|---|---|---|---|---|---|---|---|
| Stand composition (PC1) | -1.406 | -0.693 | -0.189 | -0.040 | 0.092 | 0.284 | 2.080 | 1.569 | 1.426 |
| Relative Slope Position | 0.024 | 0.269 | 0.481 | 0.503 | 0.019 | 0.770 | 1.000 | 7.397 | |
| Slope Length and Steepness factor | 2.162 | 7.444 | 9.535 | 9.698 | 0.226 | 12.056 | 16.931 | 16.744 | |
| Aspect (transformed) | 0.000 | 0.154 | 1.173 | 1.081 | 0.481 | 1.874 | 1.998 | 1.545 | 1.289 |
| Valley Depth [m] | 0.000 | 30.58 | 65.980 | 64.04 | 2.713 | 98.27 | 176.28 | 8.729 | 1.633 |
| Topographic Wetness Index | 2.135 | 3.304 | 4.273 | 4.403 | 0.079 | 5.454 | 6.692 | 11.207 | 2.206 |
| Terrain Ruggedness index | 1.040 | 2.127 | 2.621 | 2.650 | 0.050 | 3.200 | 4.612 | 30.527 | |
| Topographic Position Index | -0.679 | -0.182 | 0.005 | 0.136 | 0.034 | 0.238 | 2.168 | 2.441 | 1.739 |
| Slope [°] | 14.5 | 28.35 | 34.5 | 32.9 | 0.5 | 39.1 | 48.5 | 36.643 | 1.454 |
| Mean annual precipitation [mm] | 726.6 | 752.1 | 848.4 | 829.3 | 4.7 | 885.0 | 974.7 | 65.287 | |
| Summer precipitation [mm] | 291.1 | 298.1 | 340.0 | 339.2 | 2.2 | 363.7 | 406.5 | 55.161 | 5.028 |
| Mean annual temperature [°C] | 5.5 | 5.9 | 6.2 | 6.3 | 0.3 | 6.8 | 7.1 | 263530.5 | |
| Summer temperature [°C] | 14.8 | 15.2 | 15.6 | 15.6 | 0.0 | 16.1 | 16.6 | 114168.1 | |
| Winter temperature [°C] | -2.7 | -2.4 | -2.1 | -2.0 | 0.0 | -1.6 | -1.2 | 4413.18 | 4.887 |
| Stand density [ind. ha$^{-1}$] | 157.6 | 261.6 | 367.4 | 377.7 | 15.2 | 474.7 | 765.4 | 1.490 | 1.395 |
| Basal area [m$^2$ ha$^{-1}$] | 5.99 | 19.06 | 26.26 | 26.21 | 1.05 | 32.90 | 58.69 | 1.334 | 1.203 |

*MuMIn* package (Bartoń 2017). We developed LMMs using the *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2017) packages, while for GLMMs – the *glmmTMB* package (Brooks et al. 2017). For mortality and recruitment, where we had zero values in some cases, we included a zero-inflation component in the model, indicating the probability of a non-zero outcome.

We provided marginal means, i.e. mean outcomes from LMM for the global population (excluding random effects), to conclude about absolute effect sizes, implemented in the *emmeans* package (Lenth 2019). For continuous predictors we calculated marginal responses, i.e., prediction for each independent variable value, assuming a mean level of all other predictors and excluding random effects (i.e., for the global population), using the *ggeffects* package (Lüdecke 2018). For LMMs, we also reported marginal ($R^2_m$) and conditional ($R^2_c$) coefficients of determination, indicating the proportion of variability explained by fixed effects and both fixed and random effects, respectively (Nakagawa and Schielzeth 2013). We calculated them using the r.squarredGLMM() function from the *MuMIn* package (Bartoń 2017).

## Results

### Biomass and species composition of study plots

Total stand aboveground biomass within study plots ranged from 7.9 to 491.0 Mg ha$^{-1}$, with an average of 197.0±7.4 Mg ha$^{-1}$. Mean aboveground biomass increased from 168.0±13.0 Mg ha$^{-1}$ in 1987 through 191.8±13.0 Mg ha$^{-1}$ in 1998 to 237.4±13.0 Mg ha$^{-1}$ in 2009 (Table 2). Fixed effect explained 10.1% of variability while both fixed and random effects explained 94.7%.

**Table 2** Linear mixed-effects model of stand aboveground biomass across years, accounting for plotwise specificity as a random intercept. Model AICc=1339.7, AICc$_0$=1464.8.

| Variable | Estimate | SE | t | p | Random effect | SD |
|---|---|---|---|---|---|---|
| (Intercept) | 168.0 | 13.0 | 12.92 | <0.001 | plot | 83.64 |
| year=1998 | 23.8 | 4.5 | 5.34 | <0.001 | residual | 20.92 |
| year=2009 | 69.5 | 4.5 | 15.57 | <0.001 | - | - |

SE – standard error, t-test statistic, p – p-value, SD – standard deviation

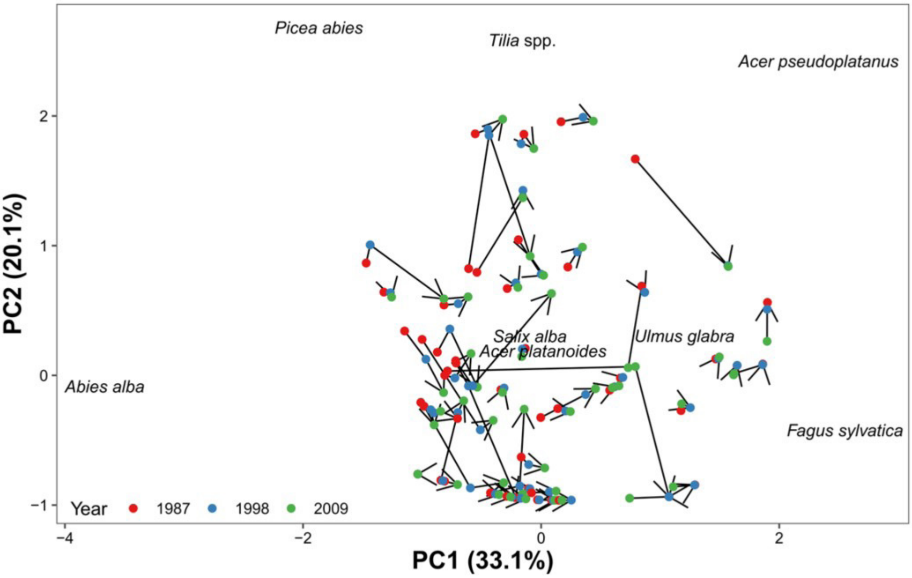

**Figure 3** Result of Principal Component Analysis of stand composition for study plots each year (n=147). Italic labels indicate species scores (for clarity, we showed only eight of the most abundant taxa). Lines connect the same study plots over time; arrows indicate the direction of change over the years.

Most studied stands were dominated by *Abies alba* or *Fagus sylvatica*; only two plots were dominated by *Picea abies* and one by *Tilia* spp. (Figure S1). Principal Components Analysis revealed that the primary gradient (PC1 axis, Figure 3) separated *Abies alba*-dominated stands from *Fagus sylvatica*-dominated. The second axis (PC2) distinguished plots with the highest proportion of both abovementioned species from stands with higher admixture of *Picea abies* (mainly in *A. alba* stands), *Tilia* spp. (in mixed *A. alba*-*F. sylvatica* stands) and *Acer pseudoplatanus* (mainly in *F. sylvatica* stands). Most study plots revealed small shifts in composition over the studied period, and most of the shifts were directed toward *F. sylvatica* forests.

## Drivers of stand biomass dynamics

The increment of studied stands ranged from 8.76 to 127.81 Mg ha$^{-1}$, with an average of 42.92±2.19Mg ha$^{-1}$, comprising from 3.89 to 41.95%, an average of 21.12±0.86% of total stand aboveground biomass. Absolute stand increment increased with topographic wetness index, winter temperature, aspect, and basal area and was higher in stands with a higher proportion of *F. sylvatica* (higher PC1 scores; Table 3, Figure 4). However, we found effects higher than their SE only for winter temperature, aspect, and basal area. Despite a lack of statistical significance, in *A. alba*-dominated stands (low PC1), we found a mean predicted increment of 45.79±7.74 Mg ha$^{-1}$, while in *F. sylvatica*-dominated (high PC1) of 38.91±8.60 Mg ha$^{-1}$. In the most north-eastern aspects, the mean predicted increment was 9.16±7.23 Mg ha$^{-1}$ lower than in the most south-western aspects. An increase in basal area by 5 m$^2$ ha$^{-1}$ raised biomass increment by 4.53±1.02 Mg ha$^{-1}$. Relative stand increment depended on basal area, stand composition, stand density, and winter temperature (Table 4; Figure 5). In *A. alba*-dominated stands (low PC1), we found a mean predicted relative increment of 0.24±0.13, while in *F. sylvatica*-dominated (high PC1) of 0.16±0.15. A gain in basal area increased relative increment from 0.30±0.12 in 10 m$^2$ ha$^{-1}$ by 0.14±0.13 in 40 m$^2$ ha$^{-1}$ to 0.08±0.20 in 60 m$^2$ ha$^{-1}$. An increase in stand density from 200 ind. ha$^{-1}$ to 700 ind. ha$^{-1}$ boosted the relative increment from 0.18±0.12 to 0.27±0.15. An increase in mean winter temperature from -2.5°C to -1.5°C caused growth of relative increment from 0.18±0.11 to 0.23±0.12. Analysis of species-specific trends revealed growing absolute increments of *F. sylvatica* and *A. alba* with increasing basal area and their proportion in stand (expressed by PC1; Table S2, Figure S2-3). Also, the absolute *A. alba* increment decreased, and the absolute *F. sylvatica* increment increased with increasing winter temperatures. Relative increments of *F. sylvatica* were raised with increasing summer precipitation. Relative increments of *A. alba* were higher in the stand with a more significant proportion and lower stand basal area (Table S3, Figure S4).

Mortality of studied stands ranged from 0.02 to 72.61 Mg ha$^{-1}$, with an average of 15.43±2.10 Mg ha$^{-1}$, comprising from 0.01 to 47.89%, an average of 8.81±1.12% of total stand aboveground biomass. Absolute stand mortality grew with basal area, slope, topographic position index, and topographic wetness index while decreased with aspect and winter temperature and was lower in stands with a higher proportion of *F. sylvatica* (higher PC1 scores; Table 3, Figure 4). However, only the effect of the basal area was higher than SE: a gain of 5 m$^2$ ha$^{-1}$ increased mortality by 3.32±0.92 Mg ha$^{-1}$. Relative mortality depended on slope, topographic wetness index, topographic position index, and winter temperature (Table 4; Figure 5). The effect of the topographic position index was weak and statistically insignificant. An increase in slope from 15° to 45° caused growth of relative mortality from 0.04±0.35 to 0.15±0.20. A boost in the topographic wetness index from 2.0 to 7.0 increased relative mortality from 0.05±0.40 to 0.15±0.30. An increase in winter temperature from -2.5°C to -1.5°C decreased relative mortality from 0.10±0.16

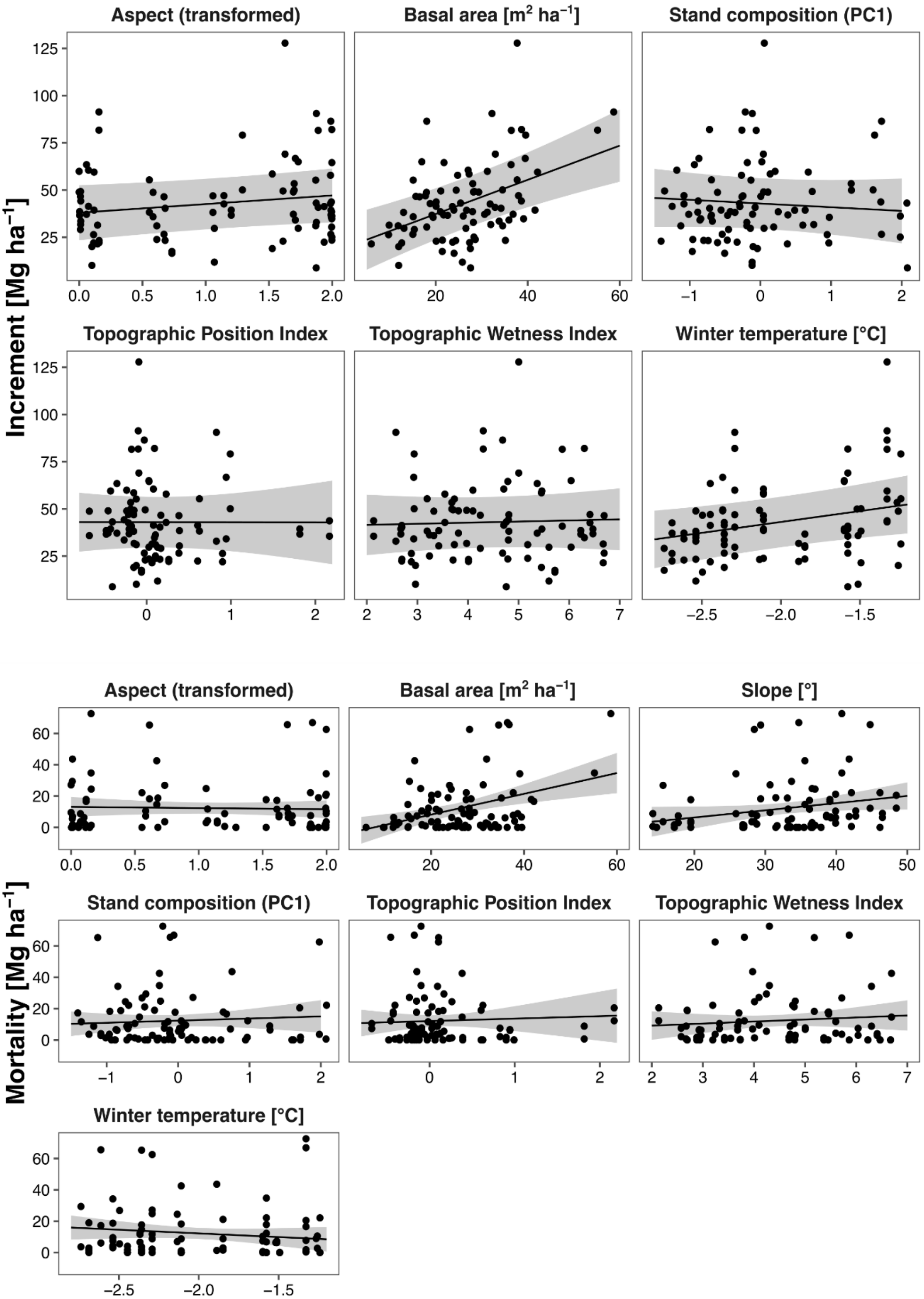

**Figure 4** Relationships between predictors and stand absolute increment and mortality (for recruitment, see Figure S2). Lines and ribbons indicated marginal responses and 95% confidence intervals, calculated from linear mixed-effects models (Table 3).

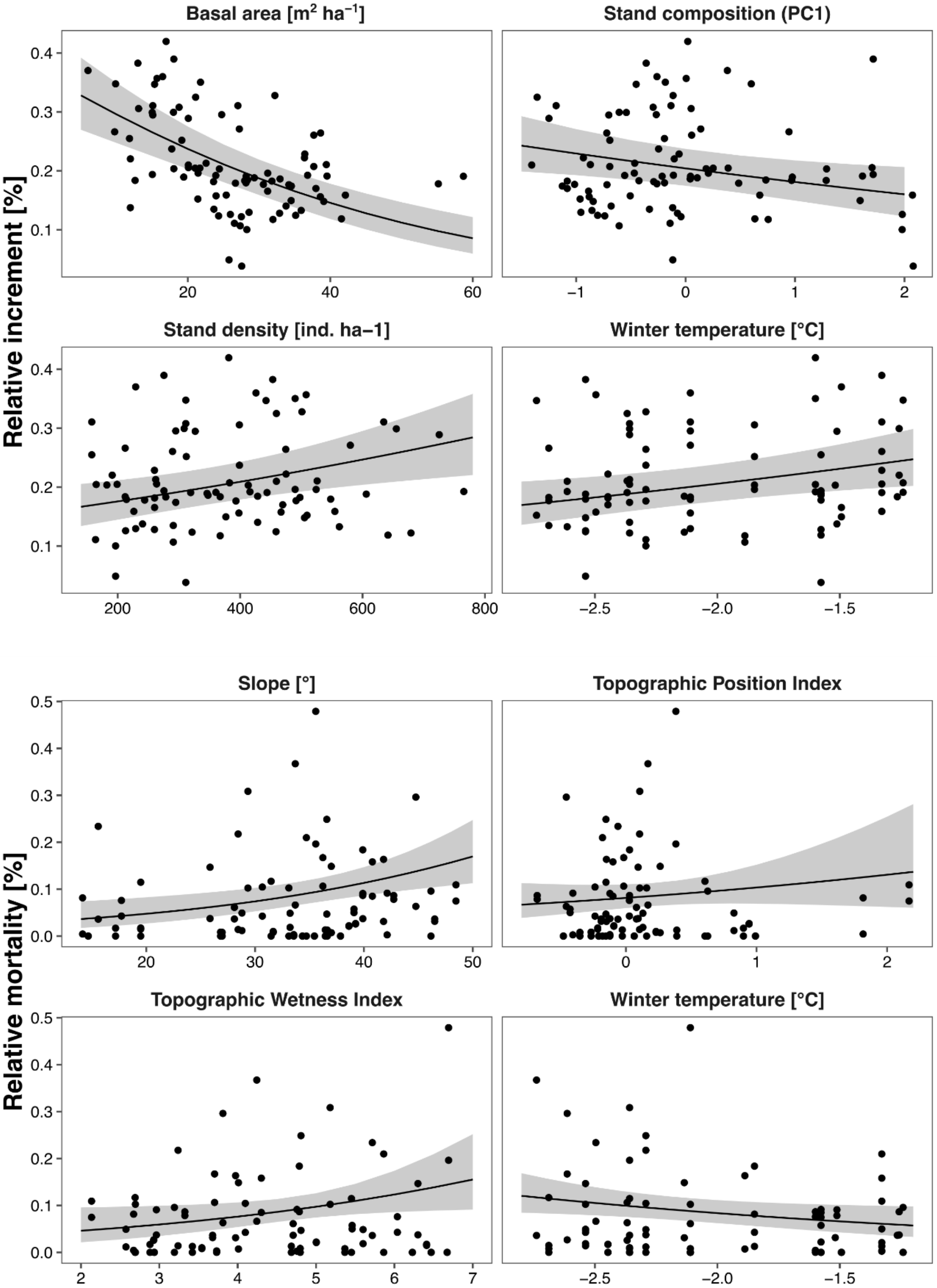

**Figure 5** Relationships between predictors and stand relative increment and mortality (for recruitment, we found the null model the best fit). Lines and ribbons indicated marginal responses and 95% confidence intervals, calculated from generalized linear mixed-effects models assuming Beta distributions (Table 4).

**Table 3** Linear mixed-effects models of stand dynamics. Abbreviations: SE – standard error, df – degrees of freedom, t – t value, Pr(>|t|) – p-value, AICc – Akaike's Information Criterion, corrected for small sample size, $AICc_0$ – AICc of null (intercept and random effects only) model, RE SD – random effect standard deviation, $R^2$m – marginal coefficient of determination, $R^2$c – conditional coefficient of determination.

| Response | Variable | Estimate | SE | df | t | Pr (>\|t\|) |
|---|---|---|---|---|---|---|
| **Absolute stand increment** | (Intercept) | 34.799 | 15.446 | 19.346 | 2.253 | 0.036 |
| plot RE SD=9.235 | Stand composition (PC1) | -1.963 | 2.640 | 38.568 | -0.743 | 0.462 |
| date RE SD=9.078 | Topographic Wetness Index | 0.593 | 1.838 | 37.083 | 0.322 | 0.749 |
| AICc=729.2<br>$AICc_0$=757.6 | Topographic Position Index | -0.050 | 4.293 | 37.101 | -0.012 | 0.991 |
| $R^2_m$=0.261; $R^2_c$=0.630 | Winter temperature [°C] | 11.549 | 4.644 | 37.706 | 2.487 | 0.017 |
| | Aspect (transformed) | 4.580 | 2.681 | 37.163 | 1.709 | 0.096 |
| | Basal area [m$^2$ ha$^{-1}$] | 0.906 | 0.203 | 40.945 | 4.460 | <0.001 |
| **Absolute stand mortality** | (Intercept) | -34.677 | 18.204 | 37.795 | -1.905 | 0.064 |
| plot RE SD=4.800 | Aspect (transformed) | -0.753 | 2.419 | 35.676 | -0.311 | 0.757 |
| date RE SD<0.001 | Basal area [m$^2$ ha$^{-1}$] | 0.663 | 0.183 | 39.042 | 3.621 | 0.001 |
| AICc=734.5<br>$AICc_0$=750.7 | Stand composition (PC1) | 1.359 | 2.387 | 36.583 | 0.569 | 0.573 |
| $R^2_m$=0.183; $R^2_c$=0.258 | Slope [°] | 0.458 | 0.233 | 36.607 | 1.968 | 0.057 |
| | Topographic Wetness Index | 1.296 | 1.740 | 35.639 | 0.745 | 0.461 |
| | Topographic Position Index | 1.563 | 4.122 | 35.665 | 0.379 | 0.707 |
| | Winter temperature [°C] | -4.675 | 4.319 | 42.617 | -1.083 | 0.285 |
| **Absolute stand recruitment** | (Intercept) | 0.418 | 6.141 | 14.671 | 0.068 | 0.947 |
| plot RE SD=1.788 | Aspect (transformed) | -0.299 | 1.508 | 39.079 | -0.198 | 0.844 |
| date RE SD=3.750 | Stand composition (PC1) | -1.037 | 1.473 | 39.913 | -0.704 | 0.486 |
| AICc=659.3<br>$AICc_0$=664.0 | Topographic Position Index | 1.030 | 2.037 | 39.022 | 0.505 | 0.616 |
| $R^2_m$=0.022; $R^2_c$=0.165 | Winter temperature [°C] | -1.949 | 2.606 | 39.826 | -0.748 | 0.459 |

to 0.07±0.23. Analysis of species-specific trends revealed growing absolute mortality of *F. sylvatica* and *A. alba* with their increasing proportion in stand (expressed by PC1; Table S2, Fig. S2-3). Also, *A. alba* mortality grew with increasing basal area. Other factors had low effect sizes and were statistically insignificant. We found higher relative mortality of *F. sylvatica* in stands with its higher proportion, and statistically insignificant effects of aspect and slope (Table S3, Figure S4). For *A. alba,* the relative mortality null model was the best fit based on AICc.

Recruitment of studied stands ranged from 0.21 to 76.00 Mg ha$^{-1}$, with an average of 7.54±1.86 ha$^{-1}$, comprising from 0.01 to 38.41%, an average of 3.99±1.00% of total stand aboveground biomass. Absolute recruitment depended on topographic position index, aspect, winter temperature, and stand composition (Table 3, Figure S5). However, all predictors were statistically insignificant. For relative stand recruitment and both absolute and relative recruitments of *A. alba* and *F. sylvatica,* we found null models as the best-fit models, according to AICc (Table 4, Figure S2-3).

**Table 4** Generalized linear mixed-effects models of stand dynamics. Abbreviations: SE – standard error, z – z value, Pr(>|z|) – p-value, AICc – Akaike's Information Criterion, corrected for small sample size, $AICc_0$ – AICc of null (intercept and random effects only) model, RE SD – random effect standard deviation, ZI – zero-inflation component.

| Response | Variable | Estimate | SE | z | Pr (>\|z\|) |
|---|---|---|---|---|---|
| **Relative stand increment** | (Intercept) | -0.380 | 0.266 | -1.429 | 0.153 |
| plot RE SD=0.205 | Stand composition (PC1) | -0.149 | 0.060 | -2.475 | 0.013 |
| date RE SD=0.123 | Basal area [$m^2$ $ha^{-1}$] | -0.030 | 0.005 | -5.971 | <0.001 |
| AICc=-230.9 | Stand density [ind. $ha^{-1}$] | 0.001 | 0.000 | 2.989 | 0.003 |
| $AICc_0$=-209.1 | Winter temperature [°C] | 0.297 | 0.112 | 2.662 | 0.008 |
| **Relative stand mortality** | (Intercept) | -6.170 | 1.286 | -4.798 | 0.000 |
| plot RE SD=0.038 | Topographic Position Index | 0.265 | 0.227 | 1.167 | 0.243 |
| date RE SD<0.001 | Winter temperature [°C] | -0.508 | 0.243 | -2.091 | 0.037 |
| AICc=-105.9 | Slope [°] | 0.047 | 0.015 | 3.090 | 0.002 |
| $AICc_0$=-100.5 | Topographic Wetness Index | 0.267 | 0.128 | 2.078 | 0.038 |
|  | ZI: (Intercept) | -1.358 | 0.264 | -5.139 | <0.001 |
| **Relative stand recruitment** | (Intercept) | -3.147 | 0.194 | -16.190 | <0.001 |
| plot RE SD<0.001 | ZI: (Intercept) | -0.228 | 0.215 | -1.064 | 0.287 |
| date RE SD<0.001 |  |  |  |  |  |
| AICc=-99.6 $AICc_0$=-99.6 |  |  |  |  |  |

# Discussion

## Shifts in stand species composition

In contrast to our first hypothesis (shifts in species composition), we found only slight changes in stand species composition over 22 years. Since 2000, stable conditions of all species distributions in Europe have been found; however, there have been some negative changes in the spatial limits of tree species (Bonannella et al. 2024). These results are consistent with our results, indicating relatively stable tree species composition of the analyzed forest ecosystems. This might be related to a low threat due to climate change predicted for dominant tree species (fir and beech) under a changing climate in the mountains (Dyderski et al. 2025) and their higher temperature requirements than Norway spruce dominating in other mountains. Most studies indicating shifts in mountain forests refer to spruce forests (Hartl-Meier et al. 2014; Bebi et al. 2017). Previous results from several mountain national parks with forest ecosystems as the dominant land cover class revealed similar trends. Although climate conditions are one of the most critical factors controlling forest growth and mortality, others also play an important role.

## Effects of stand basal area and density on forest dynamics

We found that the most important drivers of the tree aboveground biomass increment are stand composition, BA, density, and aspect (Figures 4 and 5). This is in line with hypothesis 2, assuming positive effects of both density and basal area on stand dynamics. These results, although based on a much smaller number of monitoring plots, are consistent with the results from the neighboring Tatra and Gorce National Parks (Dyderski and Pawlik 2021; Dyderski et al. 2023). We observed higher increments in *Fagus*-dominated stands, which can be attributed to the effect of growth dynamics and the higher wood density of *Fagus*. European beech is considered the most vital and competitive species in the mountains of Central Europe (Kulla et al., 2023). It has high shade tolerance, fast height growth, and low requirements on soils (Piovesan et al. 2005; Janík et al. 2016; Kulla et al. 2023; Latterini et al. 2024). In the PNP case, in *Fagus*-dominated stands, the absolute values of aboveground biomass increased with BA; however, in terms of the relative values, we observed the opposite relationship that can be associated with more intensive growth dynamics in younger stands (with lower dimensions). This finding is partly consistent with the results from the Gorce Mountains, where we also observed a relative decrease in biomass increment with increasing BA (Dyderski et al., 2023). However, modeling of the datasets from Norway, consisting of the data from thinned and unthinned experimental plots of *P. abies* indicated that gross volume increased with growing basal area up to 50 $m^2$; after that level, it became constant (Allen II et al. 2021). In addition, for the whole stand, we found a positive effect of tree density on relative increment (Figure 5).

Although unrelated to any stand-scale disturbance, the aboveground tree biomass change caused by mortality was partly controlled by several variables, among which the most important was BA. With increasing BA, mortality increased and was also slightly related to steeper slopes (Figure 5). In Switzerland, oak and beech mortality decreased with increasing DBH and tended to increase with precipitation (Rohner et al. 2012). In Sweden, beech mortality was higher in trees above 60 cm DBH (Fuentes et al. 2010). Regarding recruitment, we found it was higher in *Abies*-dominated forests, which, as mentioned above, are more shade-tolerant and grow better under the canopy but also regenerate more continuously. We did not find trends for *F. sylvatica*, and for *A. alba*, the key factors were similar to those controlling the aboveground biomass increment.

Higher tree densities indicated either younger or older stands with natural regeneration, where younger individuals expressed higher growth rates than older ones. Although these relationships are widely known (Pretzsch 2009; Jagodziński et al. 2020; Vančura et al. 2022), more interesting is a modification of these trends by aspect (Figure 5). Stand density and its changes may affect the increase in stand biomass, as was mentioned by Pretzsch (2020). The initial rapid growth of trees associated with stand-thinning treatments may increase yields, but in the long run, the trend may reverse. Jagodziński et al. (2020) proved that biomass and carbon stock of *P. abies* and *F. sylvatica* negatively correlated with stand density, and the differences between lowland and highland stand were insignificant.

The increase in the volume and biomass of a forest stand may also depend on the effect of mixing different tree species and is related to the processes of competition and facilitation (Forrester and Bauhus 2016). Lebourgeois et al. (2013) show that late summer conditions from the previous year and current summer soil water deficit and temperature significantly influenced *A. alba* growth. The study revealed higher sensitivity to temperature at higher elevations and summer drought at lower altitudes and in dry conditions. Mixing with *F. sylvatica* helped maintain higher *A. alba* growth levels during extreme climatic events and reduced its response to summer drought, especially in the driest conditions. Various facilitation processes, like changes in rooting depth, water input via stemflow, and rainfall interception, may explain the positive effects of admixture. In a different study, Hilmers et al. (2019) showed that there are differences in average periodic annual volume increment (PAI) during 30 years (1980-2010) in mixed forests with *P. abies, F. sylvatica*, and *A. alba* for all species in total and all species separately.

*F. sylvatica* (8.2 m$^3$ ha$^{-1}$ year$^{-1}$) had similar PAI during the whole period. The PAI of *P. abies* dropped significantly from 14.2 to 10.8 m$^3$ ha$^{-1}$ year$^{-1}$. *A. alba* has the opposite trend; its PAI increased from 7.2 to 11.3 m$^3$ha$^{-1}$year$^{-1}$. Significant changes in PAI (9.3 m$^3$ ha$^{-1}$ year$^{-1}$) were not observed.

### Effects of climatic and geomorphological factors on stand dynamics

Our study revealed a positive effect of winter temperatures on stand biomass increment, which is related to the positive response of beech to warming winters. This is in line with hypothesis 3, assuming the impact of climatic variables. Beech is more sensitive to frost than fir, which shaped that pattern. With warming climate conditions over the Northern Hemisphere, a significant shift in tree species distribution in the temperate forest ecosystems is expected (Reich and Oleksyn 2008; Dyderski et al. 2025; McDowell et al. 2020; Bonannella et al. 2024; Conradi et al. 2024). Although the aboveground tree biomass increase is also expected, there are deep concerns and uncertainty related to the impact of high-magnitude and high-frequency natural disturbances on forests (Thom et al. 2013; Seidl et al. 2014; Pietrzykowski and Woś 2021; Bonannella et al. 2024). Highly elevated areas of montane ranges, considered '*nowhere to go*' ecosystems, are sensitive to changes but, in the long-term perspective, can also act as adequate shelters for many plant species into the future (Loarie et al. 2009). These changes can also be significant in forest ecosystems and depend on forest canopy transmissivity for the sunlight and warm air currents (Zellweger et al. 2020).

Different experiments and empirical studies confirm the opposite impact of density on volume growth, and there are different recommendations for regulating the forest cover (Pretzsch 2009). Stand density, and its changes may affect the increase in stand biomass, as was mentioned by Pretzsch (2020). The initial rapid growth of trees associated with stand-thinning treatments may increase yields, but in the long run, the trend may reverse. Jagodziński et al. (2020) proved that biomass and carbon stock of *P. abies* and *F. sylvatica* negatively correlated with stand density, and the differences between lowland and highland stand were insignificant.

Geomorphic conditions also affected stand dynamics, as assumed in hypothesis 3. We found twice as high relative increments in SW as in NE exposition, which can be related to higher insolation (sunlight and temperature) on SW-exposed hillslopes. Although it is a generally known factor, the hillside exposition was not previously found as a good predictor of aboveground biomass increment for Polish national park forests (Dyderski and Pawlik 2020). We did not find other geomorphic agents (for instance, slope, TPI, or TWI) having such a significant impact on absolute or relative tree increment (Table 3 and 4).

Analyzing species-specific trends of stand dynamics we found the most important role of species proportion in stand biomass (Figures S3 and S5). *F. sylvatica* had higher relative increment and mortality in plots with its dominance (Figure S5), while *A. alba* absolute increment decreased (Figure S3). In the Gorce Mountains, we found a high relative change increment of *A. alba* with its growing proportion (Dyderski et al. 2023). That was also a typical behavior for *F. sylvatica* and *P. abies* in this area and the Tatra National Park (Dyderski and Pawlik 2021). *A. alba* also had higher increments on steeper slopes, with higher winter temperatures and summer precipitation (Figures S2 and S3).

## Conclusions

Understanding mechanisms of biomass dynamics in unmanaged forests is crucial due to their role in carbon retention and providing numerous ecosystem services. Using long-term permanent plots, we assessed the dynamics of *A. alba-F. sylvatica* unmanaged mountain forests over 22 years. We found that stand composition was only slightly affected across 22 years. Stand dynamics were mostly affected by stand structure characteristics, especially basal area, and density, while other factors (geomorphometric and climatic characteristics) modified these relationships. The importance of climatic and geomorphometric factors show local responses of stand dynamics, which can utilize fine-scale sites. Research on mountain forests' dynamics, besides providing us with interesting and important information about the population dynamics of trees and the impact of humans on natural processes in ecosystems, also gives us many practical tips that stakeholders can use. Monitoring the dynamics of tree stands allows us to more easily predict all threats related to natural disturbances, e.g., droughts, wind, fires, and anthropogenic ones connected with inappropriate forest management.

## Conflict of interest

The authors declare no financial or personal interests could influence the work presented in this paper.

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