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# Long-term dynamics and drivers of forest structural complexity across temperate old-growth remnants in Slovenia

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ABSTRACT

Forest structural complexity plays an important role in regulating forest functions and biodiversity habitat. A number of variables are known to influence structural complexity within forest stands across space, including tree species diversity and disturbance, yet less is known how such factors influence complexity over time. In temperate, old-growth forests, for example, a long-standing assumption is that continuous gap dynamics maintain relative stability in forest structure over time at stand scales, yet few datasets are available to test how this applies to structural complexity. We use permanent plot data spanning four decades to examine changes in plot-level structural complexity as a function of tree species diversity, disturbance, and tree recruitment, across a network of old-growth forest remnants in Slovenia dominated by mixtures of *Fagus sylvatica* and *Abies alba*. We modeled structural complexity as a function of time and plot-level covariates using Bayesian hierarchical generalized additive models. We found pronounced spatial and temporal variability in stand scale structural complexity. The results indicate that moderate severity disturbances play a role in driving temporal instability in structural complexity via mortality of canopy trees and subsequent recruitment of understory stems. We also found evidence linking higher structural complexity with the presence of *A. alba* in stands otherwise dominated by *F. sylvatica*. Emulating the large variation in complexity across space and time would require careful silvicultural planning, including prescriptions that mimic both small-scale gap dynamics, and use of variable retention harvesting to emulate moderate severity disturbances.

## 1. Introduction

Much attention has been focused on forest structural complexity as an important component of forest ecosystem functions. Higher structural complexity has been linked to increased forest resilience to disturbance (Cerioni et al., 2025; Pickering et al., 2025), net primary production (Gough et al., 2019; Hardiman et al., 2011), carbon storage (Ford and Keeton, 2017), and habitat for biodiversity (Ishii et al., 2004; Penone et al., 2019). Despite evidence that complexity of forest structures influences ecosystem functions, distinguishing the processes that drive the dynamics of complexity within forest stands is challenging (Fahey et al., 2025; Gough et al., 2022). Previous work has identified several key factors that influence structural complexity, such as tree species diversity and disturbance, yet each of these may interact and influence forest structure in different ways across spatiotemporal scales and successional stages (Gough et al., 2022).

At within-stand scales, disturbance exerts strong control on forest structural complexity through mortality of individual or patches of canopy trees, thereby promoting recruitment of younger cohorts in gaps. Moreover, disturbance can indirectly influence structure via effects on tree composition, such as through selective removal of a particular species from a stand (Cerioni et al., 2025), or by promoting tree diversity through gap size partitioning of regeneration (Busing and White, 1997; Nagel et al., 2010). Higher tree species richness within stands has been associated with more structurally complex forests. This is thought to be due to trait variation (e.g. maximum tree size and height, crown architecture, crown plasticity, and shade tolerance) among coexisting species, allowing more efficient use of resources through niche complementarity, and therefore occupation of three-dimensional canopy space (Fahey et al., 2025; Fotis et al., 2018; Juchheim et al., 2020).

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Given the idiosyncratic nature of disturbance history at local, within-stand scales, the cumulative effects of past disturbances in a stand may have strong control on contemporary forest structure and composition (Nagel et al., 2014), and therefore on structural complexity (Meigs et al., 2017).

In unmanaged forests regulated by natural processes, structural complexity is thought to reach a maximum in an old-growth stage of development (Franklin and Van Pelt, 2004; Gough et al., 2022; Zenner, 2004). Early models of forest ecosystem development suggest that old-growth forest structure is in a steady-state phase at sufficiently large stand scales (Bormann and Likens, 1979; Oliver and Larson, 1990), and this temporal stability should also apply to structural complexity. In mesic, temperate forest ecosystems, the steady-state condition in old-growth derives from relatively continuous and diffuse formation of small-scale canopy gaps. However, partial or moderate severity disturbances are also a common component of disturbance regimes in many temperate regions (Fraver et al., 2009; Janda et al., 2025; Nagel et al., 2017b; Woods et al., 2021), and contribute to the structural patterns and legacies found in old-growth stands (Meigs and Keeton, 2018; Nagel et al., 2006). These disturbances leave complex damage patterns, ranging from removal of susceptible individuals (e.g. large, old canopy trees) to larger damage patches (e.g. >0.1 ha) retaining live trees (Hanson and Lorimer, 2007; Nagel and Diaci, 2006; Woods, 2004). It is not entirely clear how these partial disturbances influence structural complexity, and effects likely vary by disturbance agent, severity, and across different spatiotemporal scales (Alveshere et al., 2025; Atkins et al., 2020; Fahey et al., 2015; Gough et al., 2022; Meigs et al., 2017). For example, complexity could be reduced over the short term if large, canopy trees are selectively removed by disturbance (Alveshere et al., 2025), whereas complexity should recover over time if gap creation leads to recruitment of small understory trees. Understanding these processes, however, requires direct long-term (e.g. multiple decades) observations of forest structural complexity, yet such studies are relatively rare in old-growth forests.

In this study, we examine the dynamics of structural complexity over time across a network of old-growth stands in temperate mountain forests of Slovenia dominated by *Fagus sylvatica* (hereafter beech), often with admixtures of *Abies alba* (fir) (Nagel et al., 2021). Following the traditional conceptual model of old-growth forest dynamics, we ask if complexity is stable over time, and if not, how do past disturbances and long-term shifts in tree species composition influence these dynamics. We take advantage of long-term monitoring of relatively large permanent plots (i.e. ~1 ha) with mapped tree locations that allow quantification of structural complexity. Four decades of observations capture a range of canopy dynamics, from continuous background mortality to occasional moderate severity disturbances, including windstorms, ice-storms, and several sites that experienced elevated levels of fir mortality due to air pollution (Nagel et al., 2021). This has caused an increasing dominance of beech across some sites due to loss of fir in the canopy and high rates of beech recruitment in the understory (Diaci et al., 2022; Nagel et al., 2019, 2015). These two late successional, shade tolerant species have very different canopy architectures - fir reaches large sizes, but has low crown plasticity, while beech is known for its crown plasticity and ability to fill canopy space when light is available (Leuschner and Ellenberg, 2017; Schroter et al., 2012). The plot network therefore provides a unique opportunity to assess how past disturbances and loss of a canopy dominant conifer influence structural complexity. We hypothesized that moderate severity disturbances prevent long-term stability of structural complexity at plot scales. Because the disturbances at our study sites typically remove larger canopy trees (Nagel et al., 2021), we predicted that moderate severity disturbances result in a short-term decline in structural complexity, but complexity should increase over time if disturbance leads to recruitment of understory trees. We also hypothesized that plots comprised of a mixture of beech and fir will have higher structural complexity than those dominated by beech.

We explore how the findings are relevant for the ecology, conservation, and management of beech dominated forests in Europe. Specifically, we discuss silvicultural tools that can emulate moderate severity disturbances to enhance structural complexity. This is especially timely given that recent strategies in Europe call for increasing structural heterogeneity and resilience in forests (European Commission, 2021), notably through the use of *closer to nature* silviculture that emulates patterns and processes found in unmanaged reference conditions (Larsen et al., 2022; Stritih et al., 2026).

## 2. Methods

### 2.1. Study area

This research was conducted in 11 old-growth forest remnants distributed throughout the Dinaric mountain range and the Southern Limestone Alps in Slovenia (Figure S1, Table S1). The sites are all located within strictly protected forest reserves, without evidence of past management, and include structures that are typical of mesic-temperate old-growth forests, including complex stand structure, canopy trees that exceed 80 cm in diameter, and large amounts of standing and lying deadwood (Nagel et al., 2017a, 2015, 2006). Tree cores collected from recently dead canopy trees across the reserves range from c. 200 – 400 years old (Nagel, unpublished data). All the sites are located within temperate-mesic mountain forests and are dominated by beech, with fir becoming codominant at some sites. Other less shade tolerant species, including *Acer pseudoplatanus* (maple) and *Picea abies* (spruce), are also abundant at some sites (Table 1). Sites in the Dinaric region are located on upper plateau positions on gentle slopes, whereas sites in the Southern Alps are located on steeper mid-slope positions. Most of the sites occur on limestone bedrock with well drained soils. Precipitation is relatively evenly distributed throughout the year, with an annual average of about 1200 mm at the driest site (DG) to > 2300 mm at the wettest sites (ZD, BV), and the mean annual temperature ranges from about 5 °C to 9 °C across the sites. A local system for evaluating site index used by the Slovenian Forest Service, which reflects both climate and soil conditions, showed relatively small variation across the plots. Subsequent analysis revealed that this index was correlated with the proportion of fir biomass across the plots (a variable used in our model), so site index was not used for further analyses.

Although there is no evidence of past management at the study sites, they have been influenced indirectly by anthropogenic drivers. Notably, fir populations across some of the study sites have experienced a long-term decline (Table 1) (Diaci et al., 2022; Nagel et al., 2019), presumably due to high levels of air pollution in the past that caused elevated mortality of adult trees. In addition to adult mortality, high population densities of ungulates have resulted in persistent recruitment failure of fir during the past four decades (Nagel et al., 2021). For example, only four fir trees recruited to a size of 5 cm dbh across all permanent plots in the current study during the entire observation period, while 89% of recruited stems were beech.

Four of the study sites captured moderate severity disturbance events during the monitoring period that caused mortality beyond typical background rates, which average about 1%/year across the study sites (Nagel et al., 2021). At the Ravna gora site (RG), a blowdown from a summer thunderstorm removed 33% of total basal area across both research plots, but most of the damage occurred in the RG2 plot. Another summer thunderstorm event in 2008 removed 28% of plot level basal area at the Menina planina site. The Bukov vrh site was damaged by an ice storm in 2014 that removed 11% of basal area across the plots. A summer thunderstorm at the Gorjanci site in 2017 removed 12% of plot level basal area. Although fir declined in abundance across most of the plots where it was present, mortality was particularly pronounced at the Pečka site (Fig. 1b,c), where annual rates of mortality reached 5.4% in the 1990s (Nagel et al., 2021). In some census intervals at the Pečka site, fir mortality was similar in magnitude to moderate severity disturbances at other sites (Table 1, Fig. 1b).

**Table 1**
Plot, census, and stand characteristics within each old-growth forest site, including data on the change in fir basal area over time and disturbance history.

| Old-growth plot | Plot area (ha) | Census years | N trees (latest census) | Basal area ($m^2$/ha) | Composition* (% basal area) | | | Fir change: BA first - last census (% change) | Disturbance (% basal area removed) |
|---|---|---|---|---|---|---|---|---|---|
| BV1 | 0.471 | 1985, 2012, 2017, 2022 | 279 | 38.5 | Fasy (88) | Acps (8) | Abal (4) | 0.6–0.7 (↑17.2%) | Ice storm 2014 (11%) |
| BV2 | 0.2025 | | 175 | 45.3 | Fasy (90) | Acps (6) | Abal (4) | 0.7–0.5 (↓24.8%) | |
| DG1 | 0.8 | 2011, 2016, 2021 | 156 | 38.2 | Fasy (98) | Acps (2) | | | |
| GO1 | 1 | 2012, 2017, 2022 | 270 | 42.3 | Fasy (98) | Acps (2) | | | Windstorm 2017 (12%) |
| KR1 | 1.1 | 1985, 2012, 2017, 2022 | 354 | 43.1 | Fasy (92) | Abal (7) | Acps (1) | 3.1–3.4 (↑7.2%) | |
| KR2 | 0.4 | | 220 | 47.3 | Fasy (83) | Abal (16) | Acps (1) | 3.6–2.9 (↓18.7%) | |
| MP1 | 0.8 | 1992, 2002, 2012, 2017, 2022 | 379 | 31 | Fasy (90) | Acps (5) | Piab (5) | | Windstorm 2008 (28%) |
| PE1 | 2.075 | 1980, 1995, 1998, 2014, 2019, 2024 | 1475 | 35.9 | Fasy (85) | Abal (15) | | 38.9–10.8 (↓72.1%) | Fir decline 1980–1998 (19.4%) |
| PE2 | 0.40 | | 303 | 42.8 | Fasy (94) | Abal (6) | | 7.7–1.0 (↓86.4%) | Fir decline 1980–1998 (12.9%) |
| PE3 | 0.425 | | 238 | 43.1 | Fasy (93) | Abal (7) | | 4.8–1.4 (↓71.2%) | Fir decline 1980–1998 (13%) |
| RR1 | 0.86 | 1984, 1994, 2010, 2015, 2020 | 709 | 56.6 | Abal (71) | Fasy (27) | Acps (2) | 43.9–34.7 (↓21.1%) | |
| RR2 | 0.80 | | 660 | 45.7 | Fasy (51) | Abal (48) | Acps (1) | 17.2–17.4 (↑1.2%) | |
| RR3 | 0.25 | | 122 | 42.9 | Fasy (70) | Abal (29) | Acps (1) | 5.0–3.1 (↓37.8%) | |
| RG1 | 0.568 | 1983, 2012, 2017, 2022 | 306 | 43.1 | Fasy (94) | Acps (6) | | | Windstorm 1983 (33%) |
| RG2 | 0.48 | | 649 | 33.7 | Fasy (59) | Acps (41) | | | |
| ST1 | 0.5 | 2000, 2012, 2017, 2022 | 227 | 46.4 | Fasy (73) | Abal (26) | Piab (1) | 5.4–6.0 (↑12.1%) | |
| SU1 | 0.862 | 1978, 1998, 2012, 2017, 2022 | 694 | 54.2 | Fasy (65) | Abal (28) | Piab (7) | 14.7–13.3 (↓9.3%) | |
| ZD1 | 0.451 | 1982, 2013, 2018, 2023 | 394 | 54.1 | Piab (95) | Fasy (5) | | | |
| ZD2 | 0.2875 | | 221 | 40.2 | Fasy (93) | Acps (6) | Piab (1) | | |

* Note: Basal area and composition were calculated from the most recent census. Species include *Fagus sylvatica* (Fasy), *Abies alba* (Abal), *Acer pseudoplatanus* (Acps), and *Picea abies* (Piab). Site names are Bukov vrh (BV), Donačka Gora (DG), Gorjanci (GO), Krokar (KR), Menina planina (MP), Pečka (PE), Rajhenavski Rog (RR), Ravna Gora (RG), Strmec (ST), Šumik (SU), and Ždrocle (ZD). Numbers correspond to plot number within each site.

### 2.2. Field measurements

Between the years 1978 and 2012, 1–3 fixed area permanent plots were established within each of the 11 old-growth sites, for a total of 19 plots overall. Plots range in size from 0.2 to 2.1 ha (mean: 0.67 ha), covering a total of 12.73 ha (Table 1). All live trees $\geq$ 5 cm diameter at breast height (dbh) are labeled with numbered aluminum tags. The plots were re-censused 2–5 times following their initial establishment, with a mean census interval length of 10 years. Since around 2010, all plots are on a 5-year re-census schedule (Table 1).

At each census, the dbh of each tagged tree was measured, trees that recruited to 5 cm dbh were tagged, stem-mapped, and recorded, and tree status was noted as alive or dead. Records of disturbance events (e.g. agent, timing, and damage patterns) that caused damage in the old-growth sites were maintained throughout the observation period (e.g. Nagel et al., 2006). The spatial coordinates of each tree were surveyed with a theodolite when plots were initially established. During subsequent censuses, the locations of new trees that recruited into the population were calculated based on the distance and azimuth from a tree mapped in the original census. Starting around 2020, all plots were re-mapped using Field-Map technology and software (IFER Ltd., Jílové u Prahy, Czech Republic), including spatial coordinates of all live and dead stems. In cases when newly mapped stem positions did not match positions from the original theodolite survey, we used the new position and back corrected these locations in the original census, including trees that died after the original mapping. Collectively, the dataset contains 7687 tagged trees.

## 3. Analyses

### 3.1. Calculation of structural complexity

To estimate structural complexity, we calculated the Structural Complexity Index (SCI) for each plot within each census interval (Zenner and Hibbs, 2000). The SCI characterizes the three-dimensional structure of live trees and is a function of both spatial tree positioning and tree size differentiation. Spatial tessellation of spatially mapped trees was used to create a triangulated irregular network (TIN) of Delaunay triangles of horizontally adjacent tree neighbors (x, y). Delaunay triangles are optimally equilateral triangles that connect each tree to its nearest neighbors. Using the diameter of each tree as the vertical (z) dimension in each triangle creates a rumpled surface that is shaped by the horizontal distribution of differentially sized trees in space. The SCI thus quantifies the cumulative dispersion of tree sizes in the entire plot by summing the local size differences of each tree to its 6–8 nearest Delaunay triangle neighbors over the entire plot. The SCI is computed as the sum of the surface areas of the TINS in three dimensions divided by the horizontal ground area covered by all triangles (Zenner, 2000). When all trees are the same size, the SCI value equals 1 (i.e., lower bound for SCI values), regardless of spatial pattern. With increasing size differences among tree neighbors, the SCI increases and indicates greater complexity; there is no upper bound to the index.

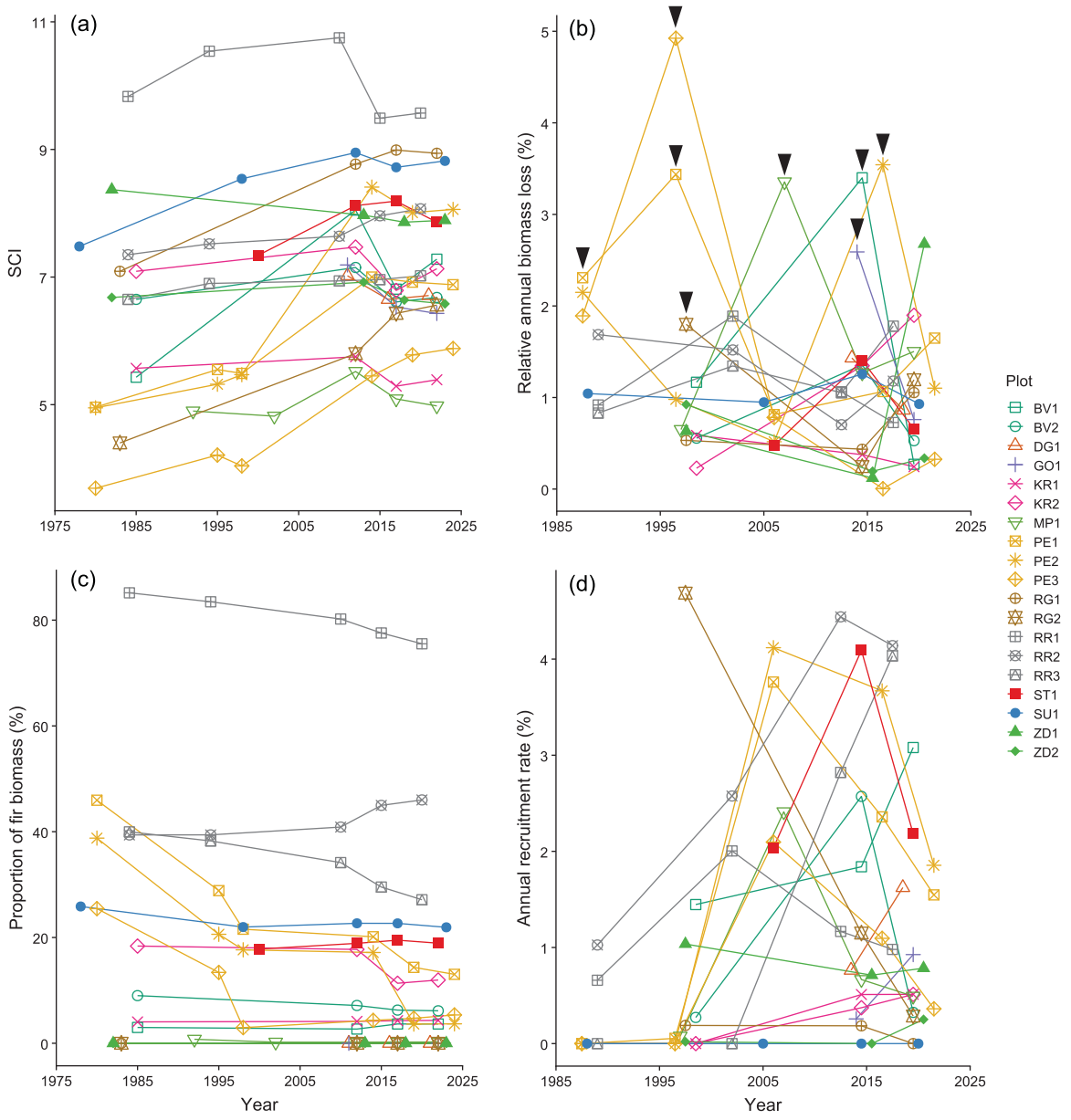



**Fig. 1.** Plot level changes in a) structural complexity (SCI), b) relative annual biomass loss (%), c) proportion of fir biomass (%), and d) annual recruitment rates (%) over time across 11 old growth forest reserves. Black arrows in panel b indicate census intervals with known disturbance events or high levels of fir mortality listed in Table 1. Note that annual rates of biomass loss and recruitment are shown at the midpoint for each census interval. Full names for the plots can be found in Table 1.

For trees close to the plot boundaries, and for which some of their nearest neighbors are likely outside of the plot boundaries, a temporary edge correction must be employed so that the TINS at the plot boundary are not distorted. To do so, trees in plots that were not perfectly aligned in a north-south orientation were first rotated around the south-western corner of the plot until the plot was in a perfect north-south / east-west orientation. This rotation keeps constant the relative positions of the trees to one another and enables the application of an edge correction (i.e., the toroidal wrap approach), which joins the top and the left of the study area to the bottom and the right, respectively (Diggle, 2003). While this avoided the distortion of Delaunay triangles near the plot boundaries, triangles that connected to a tree outside of the plot boundary were not used in the computation of the SCI to not bias results. TIN and SCI computations were done for each inventory period anew, when recruitment was incorporated and dead trees omitted from the tessellation process. Spatial tessellation and the computation of the SCI were performed in Matlab V.8.2 (Mathworks, Inc., 2013).

### 3.2. Calculation of model variables

Within each census interval for each plot, we calculated several key variables thought to influence structural complexity, including disturbance severity (as relative biomass loss), annual recruitment rates, and the proportion of fir biomass. These variables were used as fixed effects (i.e. hereafter loss, recruitment, and fir) in the models described below. We estimated the aboveground biomass of each live tree at every census based on tree dbh and species specific allometric equations provided in the *allodb* R package (Gonzalez-Akre et al., 2022). Annual biomass loss ($L_{ann}$) was then estimated using the approach outlined by Kohyama et al. (2019):

$$L_{ann} = \frac{[1-(B_{S0}/B_0)^{1/T}](B_T - B_0)}{T[(B_T/B_0)^{1/T} - 1]},$$

where T is the census interval, $B_0$ is the total biomass at time t = 0, $B_T$ is the total biomass at t = T, $B_{S0}$ is the initial biomass at t = 0 for survivors

over t = 0 to T. Compared to a simple estimate of biomass loss (i.e. ($B_0$−$B_{s0}$)/ T), this estimate is independent of census interval length and produces more reliable estimates of annual biomass loss (Kohyama et al., 2019). Given the differences in biomass across the forest reserve network due to variation in site conditions, we used relative biomass loss (%) calculated as $L_{ann}$ / $B_0$ on a per hectare basis in the statistical models described below.

To estimate recruitment, we calculated per capita annual recruitment rates for each census interval on each plot based on stem numbers. The annual recruitment rate, r, was estimated using the equation provided by Kohyama et al. (2018):

$$r = 1 - (Ns_T/N_T)^{1/T},$$

where $Ns_T$ is the number of trees from the beginning of a census interval that survived to the end of the census interval, $N_T$ is the number of trees alive at the end of the census interval $T$, and includes both surviving trees that were present in the initial census, and trees that recruited into the population during the census interval, and $T$ is the length of the census interval.

The proportion of fir biomass was used to represent the amount of fir in plot level community composition. Given the importance of large trees for structural complexity, we opted to use biomass rather than stem density. This was calculated as the total aboveground biomass of fir at the end of the census interval (T) divided by the total plot level biomass at time T.

### 3.3. Statistical analyses

We modeled SCI as a function of time and plot-level covariates using Bayesian hierarchical generalized additive models implemented in the brms package in R (Bürkner, 2018). We chose a Bayesian approach to both maintain flexibility of the modeling and to account for different sources of uncertainty, including the uncertainty in the smoothing-related parameters that are not accounted for in the standard frequentist approach (Gelman et al., 2013; Wood, 2017). We constructed two models to test our hypotheses related to disturbance and forest composition. Because fir mortality represents both a disturbance process and a compositional shift, we fitted models both with and without the proportion of fir biomass as a covariate. This allowed us to evaluate the extent to which disturbance-related biomass loss effects were potentially confounded with long-term changes in fir abundance. The base model included a smooth term for year to capture non-linear temporal trends, and the fixed effects of relative biomass loss (loss) and recruitment. A second model additionally included the proportion of fir in the stand (fir). Plot-level variation was accounted for using random intercepts and random slopes for year, allowing each plot to have its own baseline and temporal trajectory. Residual variance was allowed to vary with plot area to accommodate heteroscedasticity. All models used a Gaussian likelihood with an identity link, four Markov chains, 5000 iterations per chain (2500 warmup), and conservative sampling parameters (adapt_delta = 0.98, max_treedepth = 15) to ensure convergence. Model performance and comparison were evaluated using leave-one-out cross-validation (LOO) and ranking based on their Expected Log Predictive Density (ELPD) using the loo and loo_compare functions from the brms package in R. Posterior summaries are reported as means with 95% credible intervals. In detail, the model took the following form:

$$SCI_{it} = \beta_0 + s(t) + u_i + v_i \cdot (t - 2000) + \sum_{k=1}^{K} \beta_k \cdot X_{k,it} + \varepsilon_{it}$$

where:

- $SCI_{it}$ is the value of the SCI index at the i-th plot in the year t.
- $X_{k,it}$ is the value of k-th linearly-taken covariate at the i-th plot in the year t. Altogether, there are K covariates. In the first model (without fir) we had K= 2 and in the second model (with fir) K= 3 (loss, recruitment, and fir).
- $\beta_0$ is the (unknown) intercept
- $\beta_k$'s are (unknown) slopes corresponding to the covariates
- $u_i$ is the random (plot-specific) intercept, assuming $u_i \sim N(0, \sigma_u^2)$ with unknown $\sigma_u^2$.
- $v_i$ is the random (plot-specific) slope on time, assuming $v_i \sim N(0, \sigma_v^2)$ with unknown $\sigma_v^2$.
- $\varepsilon_{it}$ is the random error, assuming $\varepsilon_{it} \sim N(0, \exp(2 \cdot \alpha \cdot A_i))$, where $A_i$ is the area of the i-th plot and $\alpha$ is an (unknown) parameter.
- $u_i$, $v_i$, $\varepsilon_{it}$'s are assumed to be independent across i's, t's and across $u$, $v$, $\varepsilon$.
- $s(t)$ is an (unknown) continuous and smooth (potentially nonlinear) function of time. It is implemented as a complexity-penalized spline. We use the default k = 9 here.

All the unknown parameters $\beta_0$; $\beta_k$, k = 1, …, K; $\sigma_u^2; \sigma_v^2; \alpha$ (plus the unknown "functional" parameter $s(.)$) are estimated simultaneously from the data within the Bayesian estimation procedure in the Stan probabilistic environment (Carpenter et al., 2017) through the call to brm function from the brms library (Bürkner, 2018) in R (R Core Team, 2026). We used flat priors for the regression coefficients and zero-truncated t-distribution priors with 3 ° of freedom for the variance parameters (including those in the mixed-effects representation of the smooth part).

## 4. Results

Plot level SCI showed large variability over time and space, ranging from a minimum of 3.69 (PE3; 1980) to a maximum of 10.75 (RR1; 2010) (Fig. 1a). Across the most recent census in each plot (i.e. from 2020 to 2024), SCI values ranged from 4.98 (MP1) to 9.57 (RR1). We observed strong temporal dynamics in SCI for many of the plots during the last four decades. While there were some plots that showed relatively stable values of SCI over time (e.g. KR1, ZD2, RR3, ST1), most plots showed signs of non-equilibrial dynamics. Plots showing dynamic SCI trajectories were often those with a known history of moderate severity disturbance during the monitoring period, where relative annual biomass loss rates were typically > 2% in census intervals that captured disturbance (Fig. 1b). Some disturbed plots showed a decline in SCI in the census interval that captured disturbance (i.e. BV1, BV2, GO1, but not MP1), sometimes followed by a recovery in subsequent intervals. One of the plots at the Ravna gora site (RG2), which experienced a windthrow in the same year as plot establishment (1983), showed a continuous increase in SCI over time. Plots in the Pečka reserve, where elevated mortality of fir occurred during early census intervals, showed minor changes in SCI during the census intervals that captured this decline period, followed by increasing SCI values in subsequent intervals (Fig. 1a,b). One plot in Pečka (PE2) also showed a second peak in fir mortality from 2014 to 2019, which may have influenced SCI, but fir made up a small proportion of plot basal area during this interval (3.7% in 2014). Although there was large variability in annual recruitment rates over space and time, rates were often high in plots (i.e. 2–4%) that experienced past disturbance and high levels of fir mortality (Fig. 1d).

The proportion of fir (% biomass) varied from 0% to 76% across the plots in the most recent census in each plot (Fig. 1c). The plot with the highest proportion of fir (RR1) also had the highest SCI, and other sites with a high proportion of fir also had relatively high SCI values (e.g. SU1, ST1) (Fig. 2). However, it is important to note that some beech dominated plots with little to no fir also had high SCI values (e.g. RG1, BV1).

The Bayesian models provide additional insight beyond the individual plot-level observational patterns described above (Table 2,

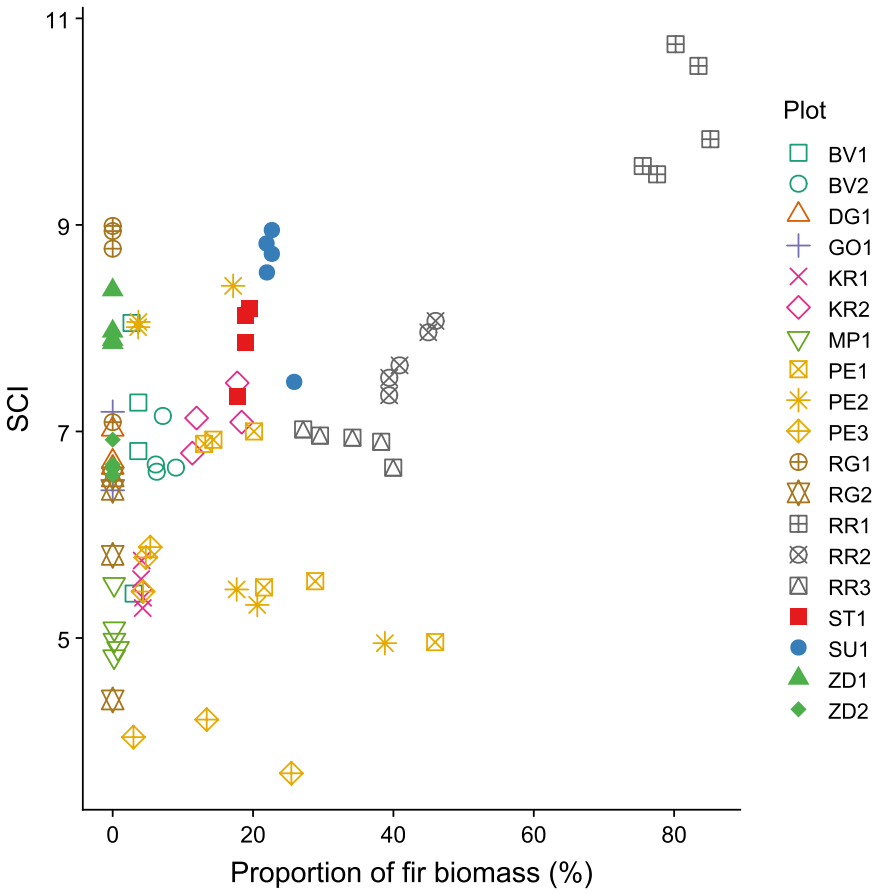



**Fig. 2.** Relationship between plot level proportion of fir biomass (%) and structural complexity (SCI) combining all census measurements over the entire monitoring period. Full names for the plots can be found in Table 1.

**Table 2**
Posterior estimates of fixed effects and variance components from Bayesian models of SCI. Posterior means and 95% credible intervals (CrI) are shown for models without and with fir. Temporal dynamics were modeled using a smooth function of year. Plot-level heterogeneity was modeled using random intercepts and random slopes for year. Residual variance was allowed to vary with plot area.

| Effect category | Parameter | Without fir (mean [95% CrI]) | With fir (mean [95% CrI]) |
|---|---|---|---|
| Fixed effects | Intercept | 6.95 [6.28, 7.62] | 6.51 [5.88, 7.13] |
| | loss | −0.12 [−0.21, −0.03] | −0.07 [−0.15, 0.01] |
| | recruitment | 0.03 [0.01, 0.05] | 0.03 [0.01, 0.05] |
| | fir | — | 0.03 [0.01, 0.05] |
| Temporal structure | Year smooth (SD) | 1.99 [0.43, 4.69] | 1.37 [0.36, 3.81] |
| Random effects standard deviations (plot) | Intercept ($\sigma_u$) | 1.37 [0.99, 1.95] | 1.17 [0.82, 1.69] |
| | Year slope ($\sigma_v$) | 0.03 [0.02, 0.04] | 0.03 [0.02, 0.05] |
| Residual variance | Area effect (log sigma) | −1.64 [−2.01, −1.27] | −1.72 [−2.05, −1.38] |

Figures S2-S5). Both models converged well (all Rhats were approximately one; high effective sample sizes), and no divergent transitions were observed. Residual variance was modeled as a function of plot size, allowing for heteroskedasticity. In the model without fir, SCI showed pronounced temporal and spatial structure. The population-level smooth term indicated a nonlinear temporal trend in SCI shared across plots after accounting for plot-specific random intercepts and linear temporal slopes (spline SD = 1.99, 95% CrI: 0.43–4.69) (Fig. 3). Across the full dataset, SCI generally increased until approximately 2010 before declining slightly in recent census periods. This smooth term represents temporal variation not fully explained by biomass loss, recruitment, or plot-level linear temporal trends. There was also pronounced heterogeneity among sites. Random intercepts varied considerably (SD = 1.37, 95% CrI: 0.99–1.95), indicating large differences in baseline SCI among sites. In addition, temporal trajectories among plots differed considerably, as indicated by variation in random slopes for year (SD = 0.03, 95% CrI: 0.02–0.04). Residual variability decreased with increasing plot size (sigma coefficient = −1.64, 95% CrI: −2.01, −1.27), confirming that larger plots exhibited lower unexplained variance.

In the model excluding fir, loss had a clear negative effect on SCI (posterior mean = −0.12, 95%, CrI: −0.21, −0.03), with posterior probability > 0.99 that the effect was negative. Recruitment showed a consistent positive effect with SCI (posterior mean = 0.03, 95% CrI: 0.01, 0.05). When fir was included as an additional predictor, it showed a positive and well-supported effect on SCI (posterior mean = 0.03, 95% CrI: 0.01, 0.05). Recruitment remained positively associated with SCI with a similar magnitude and uncertainty as in the model without fir. In contrast, the negative effect of loss was attenuated (posterior mean = −0.07, 95% CrI: −0.15–0.01), with the credible interval overlapping zero, indicating reduced independent explanatory power once the influence of fir was accounted for. This pattern suggests shared explanatory variance between loss and fir, consistent with moderate collinearity between these two variables. Inclusion of fir also reduced the variability attributed to the temporal spline and random intercepts, suggesting that

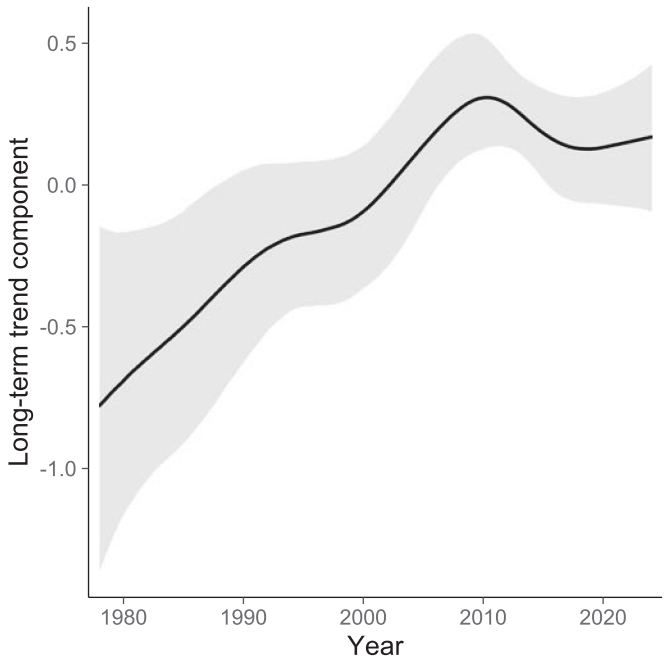



**Fig. 3.** Estimated smoothing effect of year on SCI from the Bayesian mixed-effects model without fir. The x-axis shows calendar year, and the y-axis shows the partial effect of year on SCI (on the response scale), centered at zero. The solid line represents the posterior mean of the smooth, and the shaded area indicates the 95% credible interval. The smooth describes the population-level, non-linear temporal pattern shared across plots after accounting for plot-level random effects, covariates (biomass loss and recruitment), and plot size-specific residual variance.

fir explains part of the temporal and between-site variation in SCI. Model comparison using leave-one-out cross-validation favored the model including fir. The expected log predictive density (ELPD) was higher for the fir model, with an ELPD difference of 5.3 (SE = 2.3) relative to the model without fir, indicating improved predictive performance when fir was included. Model diagnostics and random-effect summaries for the model including fir are shown in Figures S2-S5. We also explored whether the proportion of fir effect is linear or is better modeled nonparametrically, replacing the linear fir component in the original model with a spline component. Following a comparison of the two models via ELPD, we did not find evidence supporting a nonlinear fir effect (the ELPD difference is −0.3 against the nonlinear model with standard deviation 1.9).

## 5. Discussion

We found pronounced spatial and temporal variability in stand scale structural complexity across a network of old-growth temperate forest remnants located throughout mountain regions of Slovenia (Fig. 4, Figure S1). Moderate severity disturbances likely play a role in driving temporal instability in structural complexity via mortality of large canopy trees and subsequent recruitment of understory stems. We also found evidence linking higher structural complexity with the presence of fir in stands otherwise dominated by beech. Given that fir has experienced a long-term decline across some of our study sites, also acting as a disturbance, it remains difficult to tease apart disturbance and species richness effects. A clear emergent pattern, however, was that widespread recruitment by beech, driven by both disturbance and fir decline, is linked to higher structural complexity.

The SCI values found across the old-growth plot network reported here are generally in the upper range of other values found in the literature, which vary from as low as < 2 in even-aged managed conifer forests and a high as 13.34 in old-growth stands of the Pacific Northwest, USA (Peck et al., 2014; Poldveer et al., 2021; Zenner, 2004; Zenner et al., 2012). However, there are relatively few studies that quantify SCI in old-growth that provide context for comparison. For example, Zenner (2004) found values ranging from 10.5 to 13.34 in five old-growth mixed-conifer stands dominated by Douglas fir in the Oregon Cascades, yet these sites support much larger trees and stand level biomass compared to our sites. The closest comparison to our sites is from an old-growth European beech dominated forest in the Carpathian mountains, where SCI values measured across 1 ha plots ranged from 6.61 to 8.18 (Zenner et al., 2015a), and from old-growth Oriental beech




**Fig. 4.** Examples of structural complexity variation across the plot network, showing (a) a stand with very high structural complexity dominated by a mixture of fir and beech in Rajhenavski Rog (SCI ~ 10); (b) a moderatly complex pure beech stand in Gorjanci (SCI ~ 7); (c) a structurally simple beech dominated stand with a minor component of fir in Krokar (SCI ~ 5); and (d) a stand recovering from a blowdown even in 1983 at Ravna Gora (SCI ~ 4).

dominated forests in the Elborz mountains along the southern Caspian Sea that ranged from 5.89 to 7.22 (Zenner et al., 2015b). Given this limited framework for reference, the old-growth sites in this study would likely be characterized as moderately (e.g. SCI from 4 to 7) to highly complex stands (e.g. SCI from 8 to 11).

There are several important caveats that need to be addressed to help interpret our results. First, we examined structural complexity over a small number of plots, and plot sizes ranged from 0.2 to 2.1 ha, meaning that some plots were likely too small to capture a mosaic of typical canopy dynamics. Consequently, small plots were more likely to exhibit unstable SCI over time, which was also evident in the models. Certainly, larger scale plots (e.g. $>1$ ha) would be preferred to examine stand scale dynamics in structural complexity over time. Second, many of the plots are rectangular in shape, which increases edge effects when calculating the SCI. Finally, the SCI is based on tree location and diameter, data that were available throughout all census observations, yet we acknowledge that there are many other measures of structural complexity. Indeed, modern techniques based on Lidar are better at capturing the three-dimensional distribution of biomass (Atkins et al., 2023), yet studies based on repeat lidar assessments rarely extend beyond a decade (Atkins et al., 2020; Gough et al., 2022; Willim et al., 2022). In our case, the SCI provides a useful metric for tracking changes in complexity over multiple decades.

We found evidence of substantial temporal variability in SCI at the plot scale, partially supporting our first hypothesis that old-growth structural complexity is dynamic over time due to moderate severity disturbance processes. Support for this hypothesis comes from the combination of marked heterogeneity in plot trajectories from empirical evidence and the negative relationship between biomass loss and SCI identified by the Bayesian models. Scaling up to larger plots that capture a wider range of past canopy dynamics may result in more temporal stabilization, yet the moderate severity disturbances that damaged plots in this study typically caused patchy damage across entire forest reserves (e.g. ~10–50 ha) (Nagel and Diaci, 2006). These findings lend support to the idea that long-term stability at stand scales in temperate old-growth forests is rare due to periodic, moderate severity disturbances (Janda et al., 2025; Woods and Kern, 2022), which may also apply to structural complexity. It is also worth highlighting that across the entire dataset, we observed an average temporal trajectory of increasing SCI until approximately 2010 followed by a decline, suggesting that disturbance was not the only process influencing long-term changes in structural complexity. It is difficult to speculate about what processes may be driving this pattern. Because disturbances that occurred decades to centuries in the past play a role in shaping contemporary, stand-scale structural complexity (Meigs et al., 2017), one possibility is that the time window we observed here is only a snapshot of longer-term dynamics resulting from a particular history of disturbance (Woods and Kern, 2022). These patterns could also be related to ongoing climate change, whereby warming has alleviated climate constraints in mountain regions (Babst et al., 2019; Bosela et al., 2023), perhaps facilitating the recruitment and growth of beech understories across the study sites (Fig. 1d). Both of these mechanisms would require further investigation.

Assuming that high structural complexity within old-growth stands is a function of fine-scale gap dynamics, we predicted that moderate severity disturbances would initially reduce structural complexity. This was partially supported by both observations and modeling, and is likely due to removal of large canopy trees during disturbance events caused by wind and ice. However, we did not consistently observe compelling declines in SCI values following disturbances, perhaps because some of these sites have a well-developed understory of beech, such that removal of single or small groups of canopy trees may result in nearest neighbors having greater size differences after disturbance, resulting in increased SCI. The variable patterns observed in our study are not inconsistent with other research examining the short-term influence of moderate disturbance on structural complexity. Previous work documents a range of effects, including both increased or decreased complexity metrics following moderate disturbance, but results depend on disturbance characteristics (i.e. agent and severity), successional stage, and the spatial scale that metrics are computed (Alveshere et al., 2025; Atkins et al., 2020; Fahey et al., 2020; Gough et al., 2022; Meigs and Keeton, 2018). The models identified a positive link between recruitment and SCI, suggesting that disturbances indirectly influence longer term changes in structural complexity via effects on understory development. This pattern was clearly evident in the Pečka plots, where loss of large canopy fir trees from about 1980–2000 resulted in substantial increases in SCI in subsequent census intervals. These plots experienced a widespread pulse of beech recruitment following mortality in the fir population, likely driving the increase in SCI values. Increased light availability in the understory following disturbances can also promote establishment of less shade tolerant species with different crown architectures, further bolstering complexity. On our sites, for example, maple showed abundant recruitment at the RG2 plot following a windthrow in 1983 (Nagel et al., 2021).

Although the effects of fir mortality as a disturbance were difficult to separate from the species effect of fir on SCI, the Bayesian model including fir biomass indicates that fir contributes to higher levels of structural complexity. This could be due to several factors, such as the large dimensions that fir reaches at our sites, often larger than beech and sometimes $>100$ cm in dbh. Furthermore, while both species are very shade tolerant, it is possible that fir has lower mortality rates among middle story, subcanopy trees, perhaps allowing for canopy accession in very small gaps (Nagel et al., 2010), but this mechanism would need further inquiry. Finally, admixture of fir in beech dominated plots could serve to prevent beech from filling interstitial gaps in the canopy (Schroter et al., 2012), allowing more heterogeneity and light transmission to the understory. While our study does not identify these potential mechanisms, the results are consistent with research identifying positive links between local scale tree species richness and structural complexity (Ehbrecht et al., 2017; Fahey et al., 2025; Perles-Garcia et al., 2021).

## 6. Management implications

There are several important implications of our results for forest management. One is that structural complexity varies over both space and time, and this variation is something that should be emphasized when designing systems of ecological silviculture. Increasing forest structural heterogeneity at both stand and landscape scales is currently promoted under the new EU forest strategy (European Commission, 2021), particularly by employing *closer to nature* silviculture (Stritih et al., 2026). However, EU level strategies stop short of providing quantitative silvicultural guidelines for specific forest types. When possible, forest practitioners may rely on published guidelines for systems of ecological silviculture for specific forest types, which emphasize emulation of natural processes, such as moderate severity disturbance, and creation of structural complexity (See Palik and D'Amato 2023 for examples of specific forest types). This is especially important across Central Europe, where many beech dominated stands are currently in a mature phase of development with closed canopies and little structural complexity. Ecological silviculture can be used to accelerate the transition to more complex structures found in old-growth conditions. In beech dominated and mixed beech-fir forests, this should include creation of a range of gap sizes, including use of variable retention harvesting to emulate the characteristic patterns formed by moderate severity disturbances, but specific treatments will depend on initial stand conditions and development stage (Palik and D'Amato, 2023). Our findings also align well with previous studies calling for maintenance of fir within mixed mountain forests across Europe due to its important contribution to stand level productivity (Hilmers et al., 2019), perhaps suggesting a link between productivity and structural complexity when fir is present.

This work is also relevant for ongoing conservation policies in Europe. The EU's new biodiversity strategy for 2030 calls for identification and protection of existing old-growth forests (EC, 2020). The EU outlined several key indicators to facilitate the identification of old-growth conditions, mainly focused on deadwood and large-old trees, but structural complexity is also included as a complementary indicator (European Commission, 2023). Our findings highlight that old-growth can exhibit remarkable variation in structural complexity both within and across sites for a given forest community (Fig. 4). Therefore, ongoing efforts to identify old-growth should not only focus on areas with very high complexity, but should include a range of forest structural conditions.

## CRediT authorship contribution statement

**Eric K. Zenner:** Writing – review & editing, Formal analysis. **Blaž Fricelj:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Tim Pirc:** Writing – review & editing, Investigation. **Marek Brabec:** Writing – review & editing, Formal analysis. **Thomas A. Nagel:** Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

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## 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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124041.

## Data availability

Data will be made available on request.

## References

Alveshere, B.C., Stovall, A.E.L., Atkins, J.W., Gough, C.M., Fahey, R.T., 2025. Assessing the effects of disturbance severity and spatial patterning on forest canopy structure and complexity outcomes. Ecosphere 16. https://doi.org/10.1002/ecs2.70443.

Atkins, J.W., Bhatt, P., Carrasco, L., Francis, E., Garabedian, J.E., Hakkenberg, C.R., Hardiman, B.S., Jung, J., Koirala, A., Larue, E.A., Oh, S., Shao, Gang, Shao, Guofan, Shugart, H.H., Spiers, A., Stovall, A.E.L., Surasinghe, T.D., Tai, X., Zhai, L., Zhang, T., Krause, K., 2023. Integrating forest structural diversity measurement into ecological research. Ecosphere 14. https://doi.org/10.1002/ecs2.4633.

Atkins, J.W., Bond-Lamberty, B., Fahey, R.T., Haber, L.T., Stuart-Haentjens, E., Hardiman, B.S., LaRue, E., McNeil, B.E., Orwig, D.A., Stovall, A.E.L., Tallant, J.M., Walter, J.A., Gough, C.M., 2020. Application of multidimensional structural characterization to detect and describe moderate forest disturbance. Ecosphere 11. https://doi.org/10.1002/ecs2.3156.

Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P., Frank, D.C., 2019. Twentieth century redistribution in climatic drivers of global tree growth. Sci. Adv. 5, eaat4313. https://doi.org/10.1126/sciadv.aat4313.

Bormann, F.H., Likens, G.E., 1979. Catastrophic disturbance and the steady state in northern hardwood forests: a new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. Am. Sci. 67, 660–669.

Bosela, M., Rubio-Cuadrado, Á., Marcis, P., Merganičová, K., Fleischer, P., Forrester, D.I., Uhl, E., Avdagić, A., Bellan, M., Bielak, K., Bravo, F., Coll, L., Cseke, K., Rio, M. del, Dinca, L., Dobor, L., Drozdowski, S., Giammarchi, F., Gömöryová, E., Ibrahimspahić, A., Kašanin-Grubin, M., Klopčič, M., Kurylyak, V., Montes, F., Pach, M., Ruiz-Peinado, R., Skrzyszewski, J., Stajic, B., Stojanovic, D., Svoboda, M., Tonon, G., Versace, S., Mitrovic, S., Zlatanov, T., Pretzsch, H., Tognetti, R., 2023. Empirical and process-based models predict enhanced beech growth in European mountains under climate change scenarios: a multimodel approach. Sci. Total. Environ. 888, 164123. https://doi.org/10.1016/j.scitotenv.2023.164123.

Bürkner, P.-C., 2018. Advanced Bayesian multilevel modeling with the R package brms. R. J. 10, 395–411.

Busing, R.T., White, P.S., 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. Oikos 78, 562–568.

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., Riddell, A., 2017. Stan: a probabilistic programming language. J. Stat. Softw. 76, 1–32. https://doi.org/10.18637/jss.v076.i01.

Cerioni, M., Klopčič, M., Roženbergar, D., Nagel, T.A., 2025. Multiple dimensions of forest resilience to compound disturbances in a mixed sub-montane forest landscape. For. Ecol. Manag. 577, 122400. https://doi.org/10.1016/j.foreco.2024.122400.

Diaci, J., Adamic, T., Fidej, G., Rozenbergar, D., 2022. Toward a beech-dominated alternative stable state in dinaric mixed montane forests: a long-term study of the pecka old-growth forest. Front. For. Glob. Chang. 5. https://doi.org/10.3389/ffgc.2022.937404.

Diggle, P.J., 2003. Statistical analysis of spatial point patterns, 2nd edition. ed. London, UK.

EC, 2020. EU Biodiversity Strategy for 2030: Bringing nature back into our lives.

Ehbrecht, M., Schall, P., Ammer, C., Seidel, D., 2017. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agric. For. Meteorol. 242, 1–9. https://doi.org/10.1016/j.agrformet.2017.04.012.

European Commission, 2021. New EU Forestry Strategy for 2030.

European Commission, 2023. Commission guidelines for defining, mapping, monitoring and strictly protecting EU primary and old-growth forests.

Fahey, R.T., Atkins, J.W., Campbell, J.L., Rustad, L.E., Duffy, M., Driscoll, C.T., Fahey, T. J., Schaberg, P.G., 2020. Effects of an experimental ice storm on forest canopy structure. Can. J. For. Res. 50, 136–145. https://doi.org/10.1139/cjfr-2019-0276.

Fahey, C., Choi, D., Wang, J., Domke, G.M., Edwards, J.D., Fei, S., Kivlin, S.N., Larue, E. A., Mccormick, M.K., Mcshea, W.J., Phillips, R.P., Pullen, J., Parker, J.D., 2025. Canopy complexity drives positive effects of tree diversity on productivity in two tree diversity experiments. Ecology 106. https://doi.org/10.1002/ecy.4500.

Fahey, R.T., Fotis, A.T., Woods, K.D., 2015. Quantifying canopy complexity and effects on productivity and resilience in late-successional hemlock-hardwood forests. Ecol. Appl. 25, 834–847. https://doi.org/10.1890/14-1012.1.

Ford, S.E., Keeton, W.S., 2017. Enhanced carbon storage through management for old-growth characteristics in northern hardwood-conifer forests. Ecosphere 8. https://doi.org/10.1002/ecs2.1721.

Fotis, A.T., Morin, T.H., Fahey, R.T., Hardiman, B.S., Bohrer, G., Curtis, P.S., 2018. Forest structure in space and time: biotic and abiotic determinants of canopy complexity and their effects on net primary productivity. Agric. For. Meteorol. 250, 181–191. https://doi.org/10.1016/j.agrformet.2017.12.251.

Franklin, J., Van Pelt, R., 2004. Spatial aspects of structural complexity in old-growth forests. J. FORESTRY 102, 22–28.

Fraver, S., White, A.S., Seymour, R.S., 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. J. Ecol. 97, 289–298. https://doi.org/10.1111/j.1365-2745.2008.01474.x.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B., 2013. Bayesian Data Analysis, 3rd ed. Chapman and Hall/CRC (ed).

Gonzalez-Akre, E., Piponiot, C., Lepore, M., Herrmann, V., Lutz, J.A., Baltzer, J.L., Dick, C.W., Gilbert, G.S., He, F., Heym, M., Huerta, A.I., Jansen, P.A., Johnson, D.J., Knapp, N., Král, K., Lin, D., Malhi, Y., McMahon, S.M., Myers, J.A., Orwig, D., Rodríguez-Hernández, D.I., Russo, S.E., Shue, J., Wang, X., Wolf, A., Yang, T., Davies, S.J., Anderson-Teixeira, K.J., 2022. allodb: An R package for biomass estimation at globally distributed extratropical forest plots. Methods Ecol. Evol. 13, 330–338. https://doi.org/10.1111/2041-210X.13756.

Gough, C.M., Atkins, J.W., Fahey, R.T., Hardiman, B.S., 2019. High rates of primary production in structurally complex forests. Ecology 100. https://doi.org/10.1002/ecy.2864.

Gough, C.M., Atkins, J.W., Fahey, R.T., Curtis, P.S., Bohrer, G., Hardiman, B.S., Hickey, L.J., Nave, L.E., Niedermaier, K.M., Clay, C., Tallant, J.M., Bond-Lamberty, B., 2022. Disturbance has variable effects on the structural complexity of a temperate forest landscape. Ecol. Indicators 140. https://doi.org/10.1016/j.ecolind.2022.109004.

Hanson, J.J., Lorimer, C.G., 2007. Forest structure and light regimes following moderate wind storms: Implications for multi-cohort management. Ecol. Appl. 17, 1325–1340. https://doi.org/10.1890/06-1067.1.

Hardiman, B.S., Bohrer, G., Gough, C.M., Vogel, C.S., Curtis, P.S., 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology 92, 1818–1827. https://doi.org/10.1890/10-2192.1.

Hilmers, T., Avdagić, A., Bartkowicz, L., Bielak, K., Binder, F., Bončina, A., Dobor, L., Forrester, D.I., Hobi, M.L., Ibrahimspahić, A., Jaworski, A., Klopčič, M., Matović, B., Nagel, T.A., Petráš, R., del Rio, M., Stajić, B., Uhl, E., Zlatanov, T., Tognetti, R., Pretzsch, H., 2019. The productivity of mixed mountain forests comprised of Fagus sylvatica, Picea abies, and Abies alba across Europe. For. Int. J. For. Res. 92, 512–522. https://doi.org/10.1093/forestry/cpz035.

Ishii, H., Tanabe, S., Hiura, T., 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperature forest ecosystems. For. Sci. 50, 342–355.

Janda, P., Buechling, A., Svitok, M., Nagel, T.A., Mikoláš, M., Bače, R., Begović, K., Dušátko, M., Dúhová, D., Ferenčík, M., Frankovič, M., Gloor, R., Kameniar, O.,

Knír, T., Kozák, D., Lábusová, J.Á., Markuljaková, K., Pavlin, J., Petritan, I.C., Roibu, C.-C., Salerno, A.R., Ujházy, K., Veber, A., Vítková, L., Svoboda, M., 2025. Large-scale and long-term spatiotemporal patterns of disturbances in primary beech-dominated forests in the Carpathian Mountains of Europe. For. Ecosyst. 14, 100358. https://doi.org/10.1016/j.fecs.2025.100358.

Juchheim, J., Ehbrecht, M., Schall, P., Ammer, C., Seidel, D., 2020. Effect of tree species mixing on stand structural complexity. Forestry 93, 75–83. https://doi.org/10.1093/forestry/cpz046.

Kohyama, T.S., Kohyama, T.I., Sheil, D., 2018. Definition and estimation of vital rates from repeated censuses: Choices, comparisons and bias corrections focusing on trees. Methods Ecol. Evol. 9, 809–821. https://doi.org/10.1111/2041-210X.12929.

Kohyama, T.S., Kohyama, T.I., Sheil, D., 2019. Estimating net biomass production and loss from repeated measurements of trees in forests and woodlands: formulae, biases and recommendations. For. Ecol. Manag. 433, 729–740. https://doi.org/10.1016/j.foreco.2018.11.010.

Larsen, J.B., Angelstam, P., Bauhus, J., Carvalho, J.F., Diaci, J., Dobrowolska, D., Gazda, A., Gustafsson, L., Krumm, F., Knoke, T., 2022. Closer-to-Nature Forest Management. In: From Science to Policy, 12. EFI European Forest Institute.

Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests: Vegetation Ecology of Central Europe. Springer International Publishing.

Meigs, G.W., Keeton, W.S., 2018. Intermediate-severity wind disturbance in mature temperate forests: legacy structure, carbon storage, and stand dynamics. Ecol. Appl. 28, 798–815. https://doi.org/10.1002/eap.1691.

Meigs, G.W., Morrissey, R.C., Bace, R., Chaskovskyy, O., Cada, V., Despres, T., Donato, D. C., Janda, P., Labusova, J., Seedre, M., Mikolas, M., Nagel, T.A., Schurman, J.S., Synek, M., Teodosiu, M., Trotsiuk, V., Vitkova, L., Svoboda, M., 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. For. Ecol. Manag. 406, 410–426. https://doi.org/10.1016/j.foreco.2017.07.051.

Nagel, T.A., Diaci, J., Jerina, K., Kobal, M., Rozenbergar, D., 2015. Simultaneous influence of canopy decline and deer herbivory on regeneration in a conifer–broadleaf forest. Can. J. For. Res. 45, 266–275. https://doi.org/10.1139/cjfr-2014-0249.

Nagel, T.A., Diaci, J., 2006. Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. Can. J. For. Res. 36, 629–638. https://doi.org/10.1139/x05-263.

Nagel, T.A., Firm, D., Rozman, A., 2021. Intermediate disturbances are a key driver of long-term tree demography across old-growth temperate forests. Ecol. Evol. 11, 16862–16873. https://doi.org/10.1002/ece3.8320.

Nagel, T.A., Firm, D., Pisek, R., Mihelic, T., Hladnik, D., de Groot, M., Rozenbergar, D., 2017a. Evaluating the influence of integrative forest management on old-growth habitat structures in a temperate forest region. Biol. Conserv. 216, 101–107. https://doi.org/10.1016/j.biocon.2017.10.008.

Nagel, T.A., Iacopetti, G., Javornik, J., Rozman, A., De Frenne, P., Selvi, F., Verheyen, K., 2019. Cascading effects of canopy mortality drive long-term changes in understorey diversity in temperate old-growth forests of Europe. J. Veg. Sci. 30, 905–916. https://doi.org/10.1111/jvs.12767.

Nagel, T.A., Mikac, S., Dolinar, M., Klopcic, M., Keren, S., Svoboda, M., Diaci, J., Boncina, A., Paulic, V., 2017b. The natural disturbance regime in forests of the Dinaric mountains: a synthesis of evidence. For. Ecol. Manag. 388, 29–42. https://doi.org/10.1016/j.foreco.2016.07.047.

Nagel, T.A., Svoboda, M., Diaci, J., 2006. Regeneration patterns after intermediate wind disturbance in an old-growth Fagus-Abies forest in southeastern Slovenia. For. Ecol. Manag. 226, 268–278.

Nagel, T.A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecol. Appl. 24, 663–679.

Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old-growth Fagus-Abies forest of Bosnia-Herzegovina. Plant. Ecol. 208, 307–318. https://doi.org/10.1007/s11258-009-9707-z.

Oliver, C.D., Larson, B.C., 1990. Forest Stand Dynamics. McGraw-Hill, New York.

Palik, B.J., D'Amato, A.W., 2023. Ecological Silvicultural Systems: Exemplary Models for Sustainable Forest Management. Wiley.

Peck, J.E., Zenner, E.K., Brang, P., Zingg, A., 2014. Tree size distribution and abundance explain structural complexity differentially within stands of even-aged and uneven-aged structure types. Eur. J. For. Res. 133, 335–346. https://doi.org/10.1007/s10342-013-0765-3.

Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M.R., Gossner, M.M., Seibold, S., Simons, N.K., Schall, P., van der Plas, F., Manning, P., Manzanedo, R.D., Boch, S., Prati, D., Ammer, C., Bauhus, J., Buscot, F., Ehbrecht, M., Goldmann, K., Jung, K., Mueller, J., Mueller, J.C., Pena, R., Polle, A., Renner, S.C., Ruess, L., Schoenig, I., Schrumpf, M., Solly, E.F., Tschapka, M., Weisser, W.W., Wubet, T., Fischer, M., 2019. Specialisation and diversity of multiple trophic groups are promoted by different forest features. Ecol. Lett. 22, 170–180. https://doi.org/10.1111/ele.13182.

Perles-Garcia, M.D., Kunz, M., Fichtner, A., Härdtle, W., von Oheimb, G., 2021. Tree species richness promotes an early increase of stand structural complexity in young subtropical plantations. J. Appl. Ecol. 58, 2305–2314. https://doi.org/10.1111/1365-2664.13973.

Pickering, M., Elia, A., Oton, G., Piccardo, M., Ceccherini, G., Forzieri, G., Migliavacca, M., Cescatti, A., Girardello, M., 2025. Enhanced structural diversity increases European forest resilience and potentially compensates for climate-driven declines. Commun. Earth & Environ. 6, 852. https://doi.org/10.1038/s43247-025-02592-8.

Poldveer, E., Potapov, A., Korjus, H., Kiviste, A., Stanturf, J.A., Arumae, T., Kangur, A., Laarmann, D., 2021. The structural complexity index SCI is useful for quantifying structural diversity of Estonian hemiboreal forests. For. Ecol. Manag. 490. https://doi.org/10.1016/j.foreco.2021.119093.

R Core Team, 2026. R: A language and environment for statistical computing (manual).

Schroter, M., Haerdtle, W., von Oheimb, G., 2012. Crown plasticity and neighborhood interactions of European beech (Fagus sylvatica L.) in an old-growth forest. Eur. J. For. Res. 131, 787–798. https://doi.org/10.1007/s10342-011-0552-y.

Stritih, A., Lecina-Diaz, J., Mohr, J., Schattenberg, C., Ammer, C., Anselmetto, N., Bauhus, J., Bončina, A., Garbarino, M., Hlásny, T., Lindner, M., Lingua, E., Knific, E., Krüger, K., Marangon, D., Morresi, D., Mulec, K., Nagel, T.A., Potterf, M., Stritih, J., Thom, D., Welling, D., Seidl, R., 2026. Can "closer-to-nature" forest management sustain biodiversity and ecosystem services in an uncertain future? Lessons from central Europe. Curr. For. Rep. 12, 1. https://doi.org/10.1007/s40725-025-00264-6.

Willim, K., Ammer, C., Seidel, D., Annighoefer, P., Schmucker, J., Schall, P., Ehbrecht, M., 2022. Short - term dynamics of structural complexity in differently managed and unmanaged European beech forests. Trees For. People 8. https://doi.org/10.1016/j.tfp.2022.100231.

Wood, S.N., 2017. Generalized Additive Models: An Introduction With R, 2nd ed. Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279 (ed, Generalized Additive Models: An Introduction with R, Second Edition).

Woods, K.D., 2004. Intermediate disturbance in a late-successional hemlock- northern hardwood forest. J. Ecol. 92, 464–476.

Woods, K.D., Kern, C.C., 2022. Intermediate disturbances drive long-term fluctuation in old-growth forest biomass: an 84-yr temperate forest record. Ecosphere 13, e03871. https://doi.org/10.1002/ecs2.3871.

Woods, K.D., Nagel, T.A., Brzeziecki, B., Cowell, C.M., Firm, D., Jaloviar, P., Kucbel, S., Lin, Y., Maciejewski, Z., Szwagrzyk, J., Vencurik, J., 2021. Multi-decade tree mortality in temperate old-growth forests of Europe and North America: non-equilibrial dynamics and species-individualistic response to disturbance. Glob. Ecol. Biogeogr. 30, 1311–1333. https://doi.org/10.1111/geb.13291.

Zenner, E.K., 2000. Do residual trees increase structural complexity in Pacific northwest coniferous forests? Ecol. Appl. 10, 800–810. https://doi.org/10.1890/1051-0761(2000)010%5B0800:DRTISC%5D2.0.CO;2.

Zenner, E., 2004. Does old-growth condition imply high live-tree structural complexity? For. Ecol. Manag. 195, 243–258. https://doi.org/10.1016/j.foreco.2004.03.026.

Zenner, E., Hibbs, D., 2000. A new method for modeling the heterogeneity of forest structure. For. Ecol. Manag. 129, 75–87.

Zenner, E.K., Peck, J.E., Hobi, M.L., Commarmot, B., 2015a. The dynamics of structure across scale in a primaeval European beech stand. For. Int. J. For. Res. 88, 180–189. https://doi.org/10.1093/forestry/cpu042.

Zenner, E.K., Peck, J.E., Lähde, E., Laiho, O., 2012. Decomposing small-scale structural complexity in even- and uneven-sized Norway spruce-dominated forests in southern Finland. For. Int. J. For. Res. 85, 41–49. https://doi.org/10.1093/forestry/cpr052.

Zenner, E.K., Sagheb-Talebi, K., Akhavan, R., Peck, J.E., 2015b. Integration of small-scale canopy dynamics smoothes live-tree structural complexity across development stages in old-growth Oriental beech (Fagus orientalis Lipsky) forests at the multi-gap scale. For. Ecol. Manag. 335, 26–36. https://doi.org/10.1016/j.foreco.2014.09.023.