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Structural recovery but compositional shift: Eight decades of forest succession under strict protection.

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ABSTRACT

Nature reserves are expected to recreate old-growth conditions through passive succession, yet long-term, stand-wide tests are rare. We studied a hemiboreal forest in south-eastern Sweden, which has been protected since 1923. We resurveyed every tree within 10.4 ha. 88 years after the initial 1937 census, to investigate whether protection alone restores structure without eroding compositional diversity. All stems present in 1937 ($\geq$ 8.89 cm diameter at breast height, DBH) were relocated and matched to their 2025 status; all living recruits $\geq$1 cm DBH were mapped. Living stem density declined 22 % to 412 ha^{-1}, yet basal area rose 6 % to 40.7 m^2 ha^{-1} and living volume 12 % to 451 m^3 ha^{-1}. Deadwood accumulated to 190 m^3 ha^{-1}, and large living trees ($\geq$ 45 cm DBH) increased 20 % to 109 ha^{-1}. Tree species richness increased from five to thirteen, but stand dominance shifted towards shade-tolerant Norway spruce, now 62 % of stems; Scots pine density fell 40 %. Neighbourhood basal area strongly enhanced survival (odds ratio 7.8), especially for pine, whereas wetter microsites reduced survival. Recruitment (6276 stems) was 90 % spruce and concentrated where the 1937 stand had been densest; pine recruitment declined with increasing moisture. In this small reserve embedded in a managed forest landscape, strict protection rebuilt structural capital but shifted composition towards spruce dominance. Natural disturbances (windthrow, beetles) generate canopy gaps that maintain structural heterogeneity, yet outcomes are constrained by reserve size and landscape context rather than representing universal expectations for protected forests.

1. Introduction

1.1. Natural disturbance maintains structural complexity

Europe’s boreal and hemiboreal forests historically experienced recurrent surface fire, crown fire, windthrow and insect outbreaks that created multi-aged canopies, abundant coarse woody debris and veteran pines—attributes supporting thousands of disturbance-dependent fungi, beetles and birds (Kuuluvainen, 2009; Östlund et al., 1997; Siitonen, 2001). Clear-cut forestry, introduced during the twentieth century, replaced this template with even-aged, single-cohort stands that lacked deadwood and large trees (Jonsson et al., 2005; Paillet et al., 2010). The resulting structural homogenisation is considered a primary driver of the documented decline in forest biodiversity across northern Europe. (Brunet et al., 2010; Hilmers et al., 2020; Uhl et al., 2024).

1.2. Strict protection—necessary but not always sufficient

Currently, only 3 % of the EU’s land area is under strict protection, with the EU Biodiversity Strategy aiming to increase this to 10 % by 2030, including designation of remaining old-growth and primary forests for natural ecosystem processes (Gregor et al., 2024). The expectation is that harvesting cessation alone will recreate the structural hallmarks of old-growth within a century (Mason and Zapponi, 2015). However the evidence base for passive rewilding is substantial but uneven across ecosystems, response variables and spatial scales (Perino et al., 2019), and many studies rely on small, spatially implicit plots that fail to capture stem-to-stem interactions and landscape-level stochasticity (Hedwall and Mikusiński, 2016; Hytteborn et al., 2017; Janda et al., 2017). Where repeated, stand-wide inventories exist, structural recovery is rapid—coarse woody debris can reach levels comparable to those of old-growth forests within decades (Hofgaard, 1993; Shorohova et al., 2009; Unar et al., 2022). Yet these same reserves frequently

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undergo “sprucification” in hemiboreal/boreal settings: Scots pine (*Pinus sylvestris*) often gives way to shade-tolerant Norway spruce (*Picea abies*) and broadleaves (Angelstam and Kuuluvainen, 2004; Felton et al., 2020; Lindbladh et al., 2014). We note that such trajectories are typical of boreal–hemiboreal ecotones and should not be generalised to temperate broadleaf systems. Such compositional drift jeopardises taxa dependent on open, pine-dominated canopies (Kuuluvainen and Pukkala, 2024) and questions whether strict protection alone safeguards long-term biodiversity objectives.

Contemporary forest management often excludes historical disturbances, particularly fire, which have return intervals of 30–100 years in these systems. (Niklasson and Granström, 2000; Wallenius, 2011; Zackrisson, 1977), whilst facing intensifying pressures from climate-driven drought, windstorms and bark beetle outbreaks (Hlásny et al., 2022; Seidl et al., 2017). These converging factors raise critical questions about the long-term effectiveness of strict protection under novel disturbance regimes. Answering these questions requires spatially explicit, long-term data, which are exceptionally rare (Brūmelis et al., 2011; Franzén et al., 2025; Kuuluvainen and Aakala, 2011; Milberg and Strandhag, 2024).

We address this gap using wall-to-wall stem maps from 1937 and 2025 for the Säby Västerskog strict nature reserve in Sweden. This unique dataset allows a stringent test of four hypotheses:

H1. Structural recovery: Strict protection increases the number of large trees, living volume, coarse woody debris, and diameter heterogeneity to old-growth levels within one century.

H2. Sprucification: Stand composition shifts from pine dominance towards spruce and shade-tolerant broadleaves.

H3. Survival drivers: Long-term survival is jointly regulated by initial size, neighbourhood basal area, and soil moisture, with species-specific responses to disturbance.

H4. Recruitment filters: Contemporary conifer recruitment is limited by historical stand structure, and pine recruitment declines with increasing moisture.

2. Materials and methods

2.1. Study area

The study was confined to the 10.4 ha core of the Säby Västerskog strict nature reserve (58°23′N, 15°47′E; 110–145 m above sea level) in the hemiboreal zone of southeastern Sweden. The climate is temperate–continental, with a 1991–2020 normal mean annual temperature of 7.1 °C and 624 mm of precipitation (SMHI, Linköping Malmslätt weather station). Soils are coarse-textured glacial tills derived from granitic gneiss. The reserve was gazetted in 1923 and enlarged twice (today total area 22.1 ha), but all analyses herein refer to the original 10.4 ha, which has never been logged since protection. Prior use included selective felling through the mid-1800s, intermittent livestock grazing, and low-intensity slash-and-burn practices, as evidenced by charcoal layers in the soil profile. (Arnborg, 1949; Sernander, 1925). Since 1923, the stand has been affected only by natural disturbances, most recently storm “Gudrun” in 2005 (Valinger and Fridman, 2011) and a regional drought-triggered *Ips typographus* outbreak commencing in 2018 (Das et al., 2025). The current canopy is co-dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with a minor admixture of broadleaf species.

2.2. 1937 baseline inventory

In 1937, agronomist Bernhard Linder mapped all standing stems ≥3.5 imperial inches (8.89 cm) DBH across 10.4 ha using plane table surveying (1:500 scale). Conifers were classified into seven diameter classes (3.5–4, 4–8, 8–12, 12–16, 16–20, 20–24, >24 in.); broadleaves were tallied but not diameter-classed. Downed deadwood was sketched, but no standing snags were present. Dead standing trees are indicated on a contemporary map of the nearby Vessers Udde reserve (Julin, 1948), also drawn by Bernhard Linder. We therefore interpret the absence of such symbols in the Säby Västerskog map as indicating the lack of standing dead trees. We digitised the original map (Uppsala University archives), and created spatial point features for all stems. Each stem was assigned its diameter class midpoint.

2.3. 2025 resurvey

During April–May 2025, we recensused all woody stems ≥8.89 cm DBH (matching the 1937 threshold) and all living stems <8.89 cm DBH that reached a height of 130 cm to quantify regeneration. We recorded species, status (alive, standing dead, fallen dead), and DBH (nearest cm). Fallen logs were measured at breast-height equivalent along the bole. Positions were captured using Field Maps (Esri) on a smartphone with GPS (±3–5 m accuracy).

2.4. Tree matching and fate assignment

We developed a spatially explicit two-pass nearest-neighbour algorithm to link individual stems across censuses. Pass one identified survivor by matching within a 10 m radius (accommodating combined positional uncertainty), requiring species concordance and 2025 DBH ≥1937 DBH −1 cm. Pass two linked remaining 1937 stems to conspecific dead wood within a 15 m radius (accounting for fall displacement). Algorithm sensitivity was tested by varying distance thresholds (±5 m) and DBH tolerance (±2 cm), with minimal impact on results.

Unmatched 1937 stems were classified as ‘dead_missing’, and unmatched 2025 living stems were classified as ‘recruits’.

2.5. Predictor variables

Neighbourhood basal area (BA_{20}) was calculated as the summed basal area of all 1937 stems within a 20 m radius, expressed as $m^2\ ha^{-1}$ following Pommerening (2006). Individual stem volume was estimated using species-specific form factors, basal area, and height, with regional height curves from Ollas (1980) and form factors validated for southern Sweden (Näslund, 1947). The soil moisture index, derived from a national 10-m raster product that integrates depth-to-water and topographic wetness indices (with a 70:30 weighting; Anonymous, 2020). We extracted mean values within a 20-m radius of each stem as a static proxy for long-term ground wetness.

2.6. Statistical analyses

All analyses were performed in R version 4.4.3 (R Core Team, 2024) using packages car 3.1–3, sf 1.0–20, tidyverse 2.0.0, spdep 1.3–11, lme4 1.1–37, DHARMa 0.4.7, patchwork 1.3.0, and ggpattern 1.1.4. Stand-level changes in stem density, basal area, and volume between censuses were calculated per hectare, with species-specific breakdowns. Annual mortality rates were computed as m = 1 − (Nt/N0)ˆ(1/t), where N0 and Nt are initial and final stem counts over $t = 88$ years. Compositional shifts in diameter distributions were evaluated using χ^2 tests on 10-cm size classes. For survival analysis ($n = 5439$), we fitted binomial generalised linear models to test the effects of neighbourhood basal area (BA_{20}), soil moisture, species identity, and initial DBH (DBH_{1937}) on survival probability, including species × moisture and species × DBH interactions. Type II analysis of deviance assessed the significance of the predictor. Recruitment patterns were analysed using negative binomial regression with recruit counts in 40 × 40 m grid cells ($n = 87$) as the response variable, and 1937 basal area, moisture, and species as predictors. All effects are reported as odds ratios (OR, survival) or incidence rate ratios (IRR, recruitment) with 95 % confidence intervals. Spatial autocorrelation in mortality and recruitment was tested using Global

Moran's I with inverse distance weights.

3. Results

3.1. Changes in stand structure

Of the 15,253 unique dead and alive tree records assembled from the 1937 and 2025 wall-to-wall censuses, 5474 derive from the original 1937 cohort (all stems $\geq$ 8.89 cm DBH) and 9779 from post-1937 recruits (all stems > 1 cm DBH). Of the 1937 cohort, 1276 trees (23.3 % of the total) remained alive in 2025, 535 (9.8 %) persisted as standing snags or logs, and 3663 (66.9 %) had died and decomposed beyond detection. Among the 9779 recruits in 2025 (all stems > 1 cm DBH), 7740 (79.2 % of the total) were counted alive in the 2025 census, while 2039 recruits (1425 fallen, 614 standing) both recruited and died since 1937.

Based on living tree stems $\geq$ 8.89 cm DBH density declined from 525 to 412 stems ha^{-1}, with contrasting species-specific trajectories: pine decreased from 211 to 126 stems ha^{-1} (−40 %), spruce from 314 to 257 stems ha^{-1} (−18 %), while deciduous species increased from 1 to 30 stems ha^{-1} (Fig. 2a). Despite reduced stem density, living tree basal area increased by 6 %, from 38.4 to 40.7 m^2 ha^{-1}, with mean DBH increasing from 27.9 ± 12.4 cm to 31.0 ± 17.3 cm. Annual mortality rates averaged 1.2 % for pine and 2.1 % for spruce, resulting in cumulative mortality of 66 % and 84.5 % respectively. Species-specific basal area changes differed: *Pinus sylvestris* increased from 22.5 to 24.7 m^2 ha^{-1} (+10.0 %), whereas *Picea abies* remained relatively stable (15.9 → 15.6 m^2 ha^{-1}, −2.1 %). Living volume increased 12 % (402 → 451 m^3 ha^{-1}): pine accounted for most of the gain (246 → 288 m^3 ha^{-1}), spruce remained stable (156 → 159 m^3 ha^{-1}), and deciduous species contributed 3 m^3 ha^{-1} by 2025 (Fig. 2b). Deadwood reached 190 m^3 ha^{-1} (208 stems ha^{-1}), dominated by spruce (113 m^3 ha^{-1}) and pine (62 m^3 ha^{-1}). (See Fig. 1.)

3.2. Size class shifts and large trees

Among living trees, *P. abies* stems declined by 18 % (3253 → 2668) while mean DBH increased marginally from 22.9 to 24.3 cm. The diameter distribution remained strongly skewed towards smaller size classes, with the modal class staying at 10–19 cm in both censuses (52.7 % in 1937, 45.8 % in 2025), though the distribution showed a slight flattening ($\chi^2(8) = 90.8$, $p < 0.001$; Fig. 3a). Notably, spruce expanded into larger size classes absent in 1937, with trees now reaching 70–100 cm DBH. *P. sylvestris* experienced more dramatic changes, with numbers falling 40 % (2186 → 1302), but surviving individuals grew markedly larger (mean DBH 35.4 → 49.0 cm). The diameter distribution underwent a complete transformation: small trees (10–29 cm) decreased from 29.8 % to just 2.5 %, while the modal class shifted from 30 to 39 cm (39.0 %) to 50–59 cm (36.3 %), indicating strong selection for larger individuals ($\chi^2(8) = 1286.8$, $p < 0.001$; Fig. 3b). Pine also expanded its maximum size from 62 cm to 96 cm DBH. Density of large living trees ($\geq$45 cm DBH) rose from 91.0 → 109.2 ha^{-1} (+20 %), driven chiefly by pine (+203 stems) with a slight spruce decline (−17). Large-diameter trees provide disproportionate habitat value and dominate above-ground carbon pools, underscoring their conservation significance.

The total dead wood pool comprised 2156 stems (208 ha^{-1}), with markedly different size distributions between size cohorts (Fig. S3). Trees from the 1937 cohort that died by 2025 ($n = 535$) exhibited a bell-shaped distribution, peaking at 30–39 cm DBH, whereas newly recruited dead trees ($n = 1621$) were strongly skewed towards smaller size classes, with 54.6 % falling within the 10–29 cm range.

Large dead trees ($\geq$45 cm DBH) totalled 303 stems (29.2 ha^{-1}), with 62 % recruited after 1937 (18.1 ha^{-1}) versus 38 % from the original cohort (11.1 ha^{-1}). Species composition of large dead wood was dominated by spruce (62.0 %, 18.1 ha^{-1}), followed by pine (33.3 %, 9.7 ha^{-1}). Mean DBH of large dead trees was remarkably similar

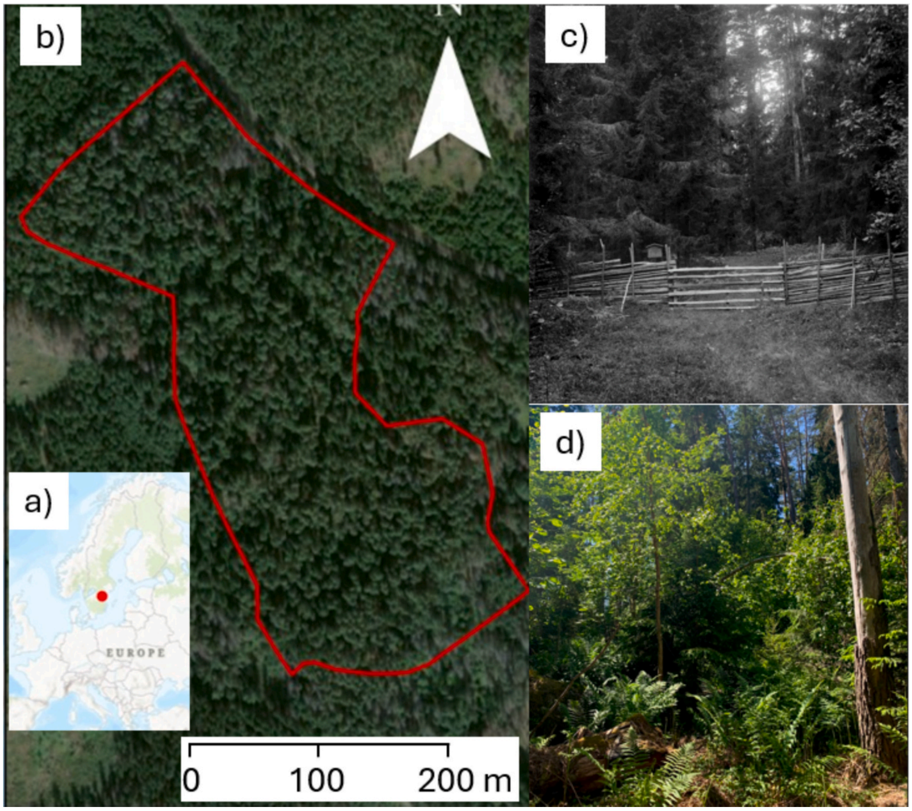

Fig. 1. Study location (a) and 2022 satellite image (b) of Säby Västerskog; oblique photographs from the same vantage point in 1924 (c) and 2025 (d). Photo credits JE Thorin (1862–1930) and Emil Ideskär.

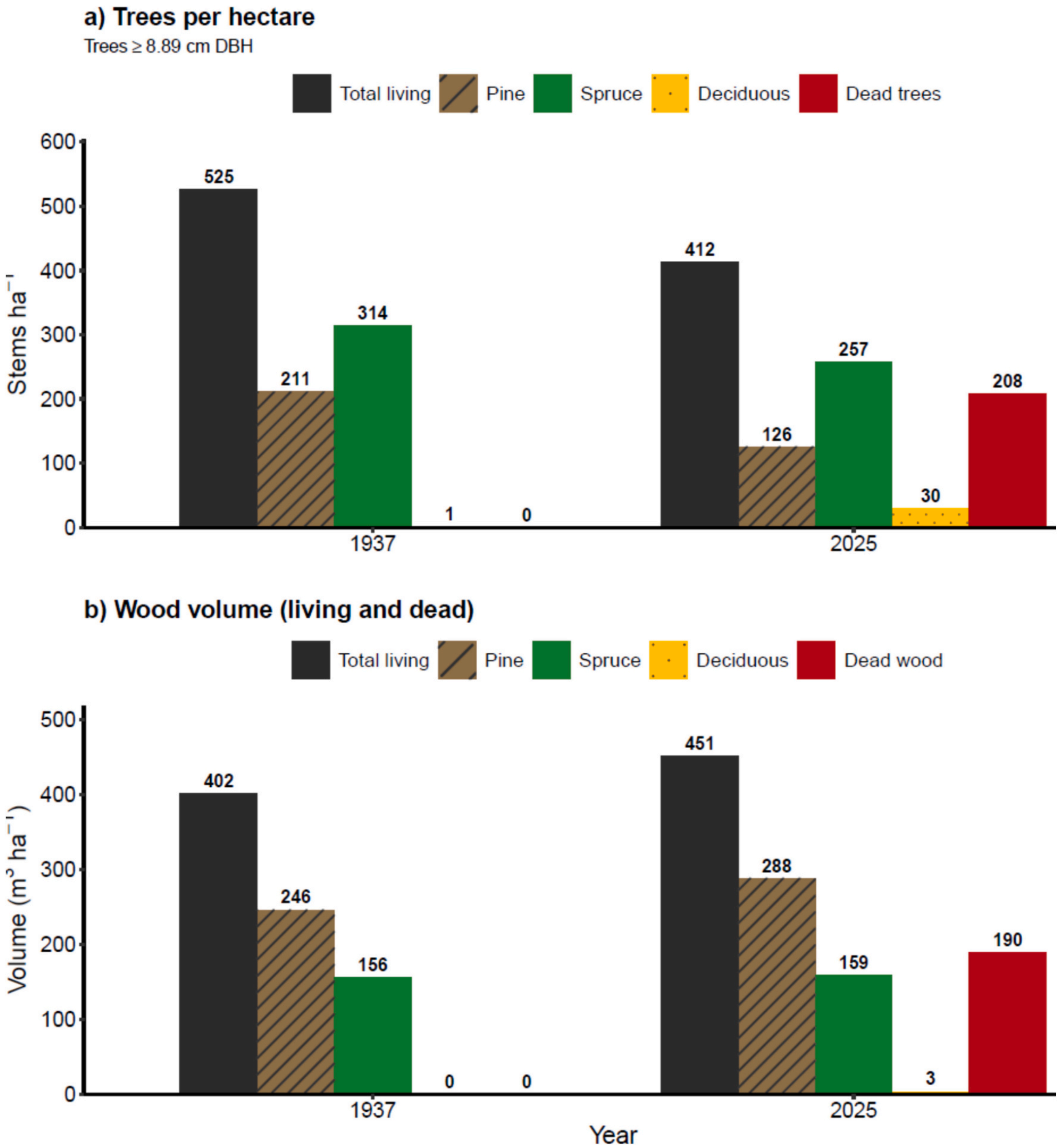

Fig. 2. Changes in forest structure between 1937 and 2025 showing: (a) Stem density (stems ha^{-1}) and (b) wood volume (m^3 ha^{-1}) by species group for all trees ≥8.89 cm DBH. Dark grey bars represent total living trees, with species-specific contributions shown for Scots pine (*Pinus sylvestris*, brown with diagonal stripes), Norway spruce (*Picea abies*, solid green), and deciduous species (golden yellow with circles). Dead trees and dead wood (solid dark red) include both standing dead and fallen dead wood. In 1937, no dead trees were recorded in the inventory. Total living stem density decreased from 525 to 412 stems ha^{-1} (−22 %), whilst total living wood volume increased from 402 to 451 m^3 ha^{-1} (+12 %). Dead wood accumulated to 208 stems ha^{-1} and 190 m^3 ha^{-1} by 2025, representing 34 % of total stem density and 30 % of total wood volume. Thus, spruce remained dominant by stems, pine accounted for most volume and its increase. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between cohorts (52.5 cm for 1937 trees, 52.7 cm for recruited trees), though maximum sizes reached 90 cm DBH.

3.3. *Species composition and richness*

Living tree richness increased from five to thirteen species between censuses. *P. abies* now constitutes 62 % of living stems, *P. sylvestris* 30 %, and broad-leaved taxa collectively 8 %. Colonisers absent in 1937 were, for instance, *Sorbus aucuparia* (41 stems in total), *Corylus avellana* (30) and *Salix caprea* (6)—signalling diversification towards a mixed conifer–broadleaf late-successional forest. We caution that this diversification co-occurs with reduced pine recruitment.

3.4. *Growth of surviving trees*

For the 1248 conifers alive and measured in both years (504 spruce, 744 pine), mean annual DBH growth was 0.17 ± 0.13 cm yr^{-1}, equivalent to a radial increment of 0.85 ± 0.63 mm yr^{-1}. A linear model revealed significant effects of initial DBH ($F = 140.2$, $p < 0.001$), species ($F = 70.9$, $p < 0.001$), and their interaction ($F = 34.0$, $p < 0.001$), explaining 12.3 % of variation (adjusted $R^2 = 0.121$). The species × DBH interaction reflected contrasting growth strategies (Fig. 4). Pine exhibited a strong size-dependent growth decline, with small trees (10–20 cm DBH) averaging 0.37 ± 0.12 cm yr^{-1}, but large trees (50–70 cm DBH) averaged only 0.14 ± 0.13 cm yr^{-1}. In contrast, spruce maintained relatively constant growth across size classes

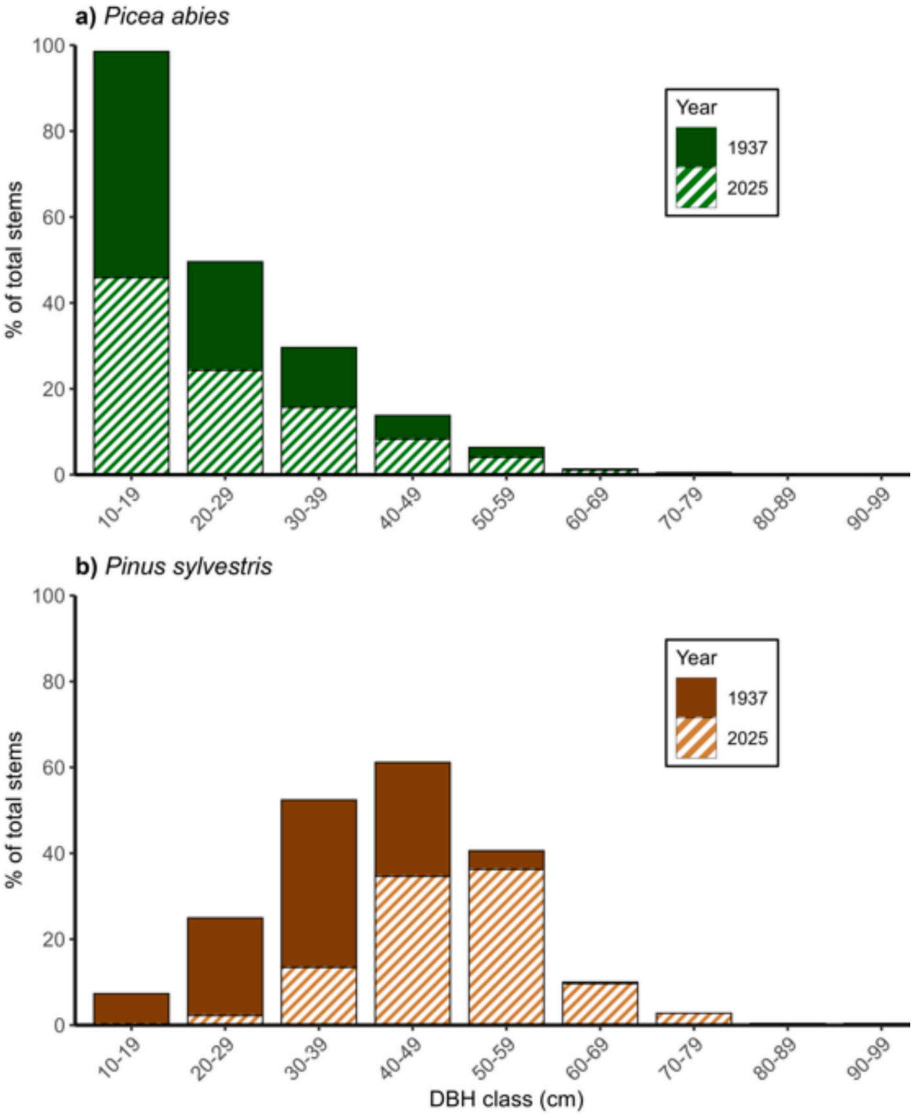

Fig. 3. Diameter-class distributions (10 cm bins) of living stems for (a) *Picea abies*; (b) *Pinus sylvestris*. Stacked bars show the percentage distribution across size classes for 1937 (solid fill) and 2025 (diagonal stripes).

(0.17 ± 0.14 cm yr^{-1}), with minimal size dependence ($R^2 = 0.005$ vs 0.243 for pine). The growth curves intersected at approximately 35 cm DBH; below this threshold, pine grew faster, while above it, spruce dominated. Maximum annual DBH increments reached 0.78 cm yr^{-1} (3.9 mm yr^{-1} radial) in pine and 0.74 cm yr^{-1} (3.7 mm yr^{-1} radial) in spruce, values consistent with those reported for temperate conifer stands of similar age.

Of the 5474 stems present in 1937, 1248 (22.9 %) survived to 2025, while 4191 died. Type II analysis of deviance revealed that neighbourhood basal area was the strongest predictor of survival (LR $\chi^2(1) = 2849.9$, $p < 2.2 \times 10^{-16}$), followed by species identity (LR $\chi^2(1) = 39.3$, $p = 3.7 \times 10^{-10}$) and soil moisture (LR $\chi^2(1) = 18.9$, $p = 1.4 \times 10^{-5}$). Two significant interactions emerged: species × DBH (LR $\chi^2(1) = 8.9$, $p = 0.003$) and species × basal area (LR $\chi^2(1) = 5.1$, $p = 0.024$) (Table 1). The main effect of moisture showed that survival decreased significantly with wetter conditions (coefficient $= -0.242$, SE $= 0.057$, $p < 0.001$), indicating that trees in drier microsites had better long-term survival. The species × DBH interaction revealed contrasting size-dependent survival patterns: while spruce showed declining survival with increasing size (coefficient $= -0.020$, SE $= 0.008$, $p = 0.014$), pine showed the opposite trend, with larger trees having better survival (interaction coefficient $= 0.033$, SE $= 0.011$, $p = 0.003$). The species × basal area interaction indicated that both species benefited from having neighbours in 1937 (main effect coefficient $= 2.049$, SE $= 0.078$, $p < 0.001$), but this positive effect was even stronger for pine (interaction coefficient $= 0.260$, SE $= 0.116$, $p = 0.025$). These patterns are illustrated in Fig. 5. Spatial analysis revealed significant mortality clustering for both species (Global Moran's $I = 0.077$ for *Picea abies*, $I = 0.032$ for *Pinus sylvestris*; both $p \leq 0.001$), with spruce showing 2.4-fold stronger spatial aggregation than pine (Fig. S2a–b).

3.5. Recruitment patterns (all sizes)

Across the 87 40 × 40 m grid cells, 6276 recruits were recorded: 90.1 % spruce, 6.8 % pine, 3.1 % broadleaves. Recruitment increased with 1937 basal area (spruce: IRR = 1.23, 95 % CI: 1.15–1.31; pine: IRR = 1.31, 95 % CI: 1.18–1.45 per additional 1 m^2 ha^{-1}) and declined with moisture for pine (IRR = 0.985, 95 % CI: 0.971–0.999) but not spruce ($p = 0.42$) (Table 2). Recruitment counts were spatially clustered (Moran's $I = 0.27$, $p < 0.001$) (Fig. S2c–d). These legacies underscore that current patterns are contingent on past structure and local edaphic conditions.

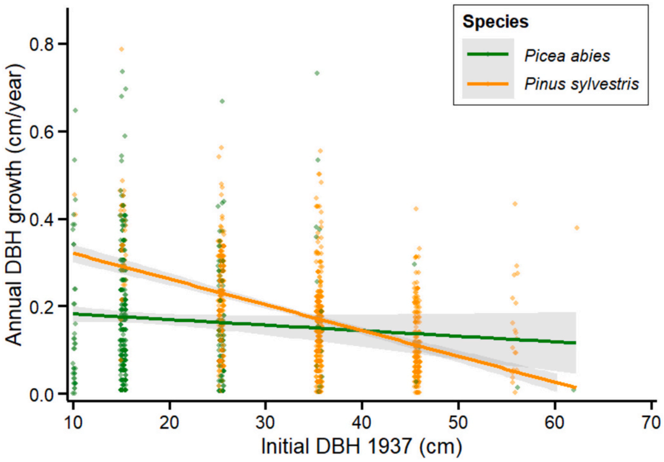

Fig. 4. Annual DBH growth (1937–2025) as a function of initial DBH for surviving *Picea abies* (green) and *Pinus sylvestris* (orange); $n = 1248$ trees. Lines show linear model predictions; shaded ribbons are 95 % confidence intervals. The significant species × initial DBH interaction ($F = 34.0, p < 0.001$) indicates contrasting size–growth relationships, where pine growth declined steeply with increasing size (from 0.37 to 0.14 cm yr^{-1}). In comparison, spruce maintained relatively constant growth across all size classes (0.17 ± 0.14 cm yr^{1}). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Generalised linear model results for tree survival from 1937 to 2025. Model coefficients are on the log-odds scale (± SE), with odds ratios and 95 % CIs. Baseline species = *Picea abies*; Neighbourhood basal area (BA_{20}, log-transformed) and moisture are centred and scaled; DBH in cm. Generalised linear model with binomial error and logit link; response = alive (1) or dead (0) in 2025.

Predictor	Estimate ± SE (log odds)	Odds ratio (95 % CI)	p
(Intercept)	−2.091 ± 0.190	0.124 (0.085–0.180)	< 0.001
DBH 1937 (cm)	−0.020 ± 0.008	0.980 (0.965–0.996)	0.014
BA_{20} (log-transformed)	2.049 ± 0.078	7.763 (6.662–9.046)	< 0.001
Moisture (scaled)	−0.242 ± 0.057	0.785 (0.702–0.878)	< 0.001
Pinus sylvestris	−0.267 ± 0.347	0.766 (0.388–1.512)	0.442
DBH × *Pinus sylvestris*	0.033 ± 0.011	1.034 (1.011–1.057)	0.003
BA_{20} × *Pinus sylvestris*	0.260 ± 0.116	1.297 (1.034–1.628)	0.025

4. Discussion

4.1. Structural recovery with compositional divergence

Our 88-year dataset from the 10.4-ha Säby Västerskog reserve demonstrates that in this specific case, strict protection rapidly restored old-growth structural attributes, confirming H1. Living volume increased 12 % to 451 m^3 ha^{-1}, deadwood accumulated to 190 m^3 ha^{-1}—matching Baltic virgin forest medians (Nilsson et al., 2002; Shorohova and Shorohov, 2001)—and large trees (≥45 cm DBH) increased 20 % to 109 ha^{-1}. This structural recovery within one human lifetime demonstrates, in this reserve, the capacity of passive succession to rebuild forest capital under strict protection (Mason and Zapponi, 2015). However, this structural success masked profound compositional change. Spruce now constitutes 62 % of living stems despite stable basal area, while pine declined 40 % in stem density. It is important to note that 1937 does not represent an equilibrium or a "baseline"; rather, we interpret change relative to that documented inventory, acknowledging that disturbance history has likely modulated variability in composition.

Tree-species richness more than doubled (from five to thirteen taxa), reflecting colonisation by broad-leaved pioneers (e.g. *Salix* spp. and *Sorbus aucuparia*) that establish in the new gap mosaic (Whitmore, 1989). The diameter distributions reveal contrasting trajectories: spruce-maintained recruitment across all size classes with its mode remaining at 10–19 cm, whereas pine distribution shifted dramatically from 30 to 39 cm to 50–59 cm, indicating recruitment failure. This "sprucification" validates H2 and mirrors patterns in other Fennoscandian reserves where fire exclusion enables shade-tolerant species to dominate (Angelstam and Kuuluvainen, 2004; Hedwall and Mikusiński, 2016; Kuuluvainen, 2009; Lindbladh et al., 2014). Compositional drift represents a fundamental alteration in habitat quality for pine-associated biodiversity (Kuuluvainen and Pukkala, 2024), challenging the assumption that structural metrics alone indicate conservation success. Our results suggest that within a small, strictly protected reserve where characteristic landscape-scale disturbance cannot operate, strict protection coincided with structural recovery, yet a compositional shift towards shade-tolerant conifers. We do not infer that strict protection generally yields similar outcomes across temperate, hemiboreal or boreal forests; responses are expected to vary with reserve size, landscape context and disturbance regime (cf. Janda et al., 2017; Kuuluvainen and Aakala, 2011; Seidl et al., 2017).

4.2. Mechanistic drivers of forest dynamics

Contrary to expectations (H3), neighbourhood density emerged as a positive predictor of survival, with trees having neighbours in 1937 showing dramatically higher survival than isolated individuals (coefficient = 2.049, $p < 0.001$). This counterintuitive positive neighbourhood effect likely reflects site-quality and microclimatic buffering rather than direct demographic facilitation, consistent with context-dependent survival processes. The significant species × basal area interaction (coefficient = 0.260, $p = 0.024$) indicated that pine benefited more from neighbours than spruce, possibly through facilitation or shared mycorrhizal networks (Simard et al., 2012). Moisture emerged as a significant negative predictor of survival (coefficient = −0.242, $p < 0.001$), with trees in drier microsites showing better long-term persistence. This suggests that, in the absence of fire, wet conditions may promote root pathogens or create anoxic soil conditions that are detrimental to survival (Lindbladh et al., 2014). The species × size interaction (coefficient = 0.033, $p = 0.003$) revealed contrasting survival strategies: while spruce showed declining survival with increasing size, larger pines had significantly better survival, likely due to their emergent crown architecture, which allowed them to access light above the spruce canopy. This size-dependent mortality contributed to the spatial clustering observed (Moran's $I = 0.077$ for spruce), generating the coarse woody debris critical for saproxylic communities; 62 % of large dead trees (≥45 cm) were recruited after 1937.

Contemporary recruitment patterns (H4) demonstrated strong historical legacies, with each 1 m^2 ha^{-1} of 1937 basal area increasing recruitment by 23 % (for spruce) and 31 % (for pine). Critically, pine recruitment declined with soil moisture (IRR = 0.985) while spruce showed no moisture response, explaining the 90 % spruce dominance among 6276 recruits. This differential response to edaphic conditions, combined with fire absence, fundamentally constrains pine regeneration to increasingly rare microsites (Karlsson and Örlander, 2000; Linder et al., 1997).

The generality of this case is constrained by reserve size (10.4 ha) and its managed-forest matrix. In small, isolated reserves, natural disturbances rarely manifest at their characteristic spatial scales, and edge-to-core feedbacks with surrounding stands can alter successional pathways. Recognising these constraints clarifies why our structural and compositional trends should be interpreted as context-dependent rather than biome-wide patterns and motivates scale-appropriate implications (Niklasson and Granström, 2000). Nevertheless, natural disturbances remain important drivers of forest structure within the reserve.

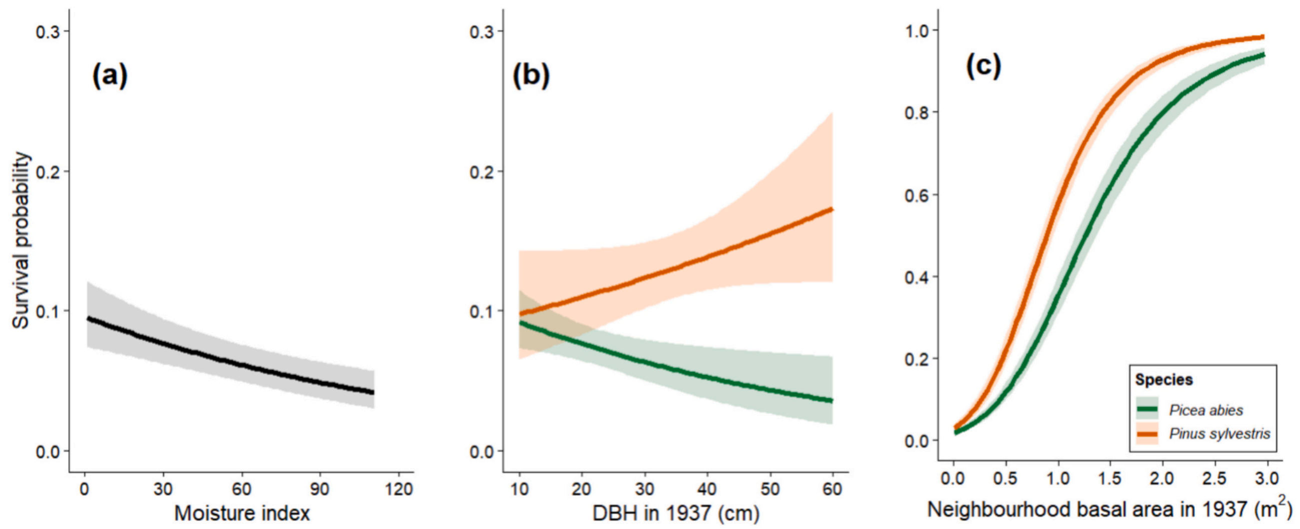

Fig. 5. Predicted effects on tree survival probability (1937–2025). (a) Main effect of moisture index on survival probability for *Picea abies* (baseline species), holding other covariates at their means. (b) Interactive effect of initial tree size (DBH 1937) and species on survival probability. (c) Interactive effect of neighbourhood basal area (log-transformed) and species on survival probability. Shaded areas represent 95 % confidence intervals. In panels (b) and (c), green lines represent *Picea abies* and orange lines represent *Pinus sylvestris*. Based on a generalised linear model with binomial error distribution ($n = 5439$ trees). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Environmental drivers of tree recruitment. (a) *Picea abies* (Norway spruce).

Parameter	Coefficient (s. e.)	Rate ratio	95 % CI	z	p
Intercept	3.141 (0.270)	23.124	13.616–39.269	11.62	< 0.001
Basal area 1937 (m^2 ha^{-1})	0.207 (0.035)	1.230	1.148–1.319	5.86	< 0.001
Moisture index	−0.001 (0.003)	0.999	0.993–1.005	−0.29	0.775

(b) *Pinus sylvestris* (Scots pine)

Parameter	Coefficient (s. e.)	Rate ratio	95 % CI	z	p
Intercept	1.225 (0.243)	3.404	2.113–5.485	5.04	< 0.001
Basal area 1937 (m^2 ha^{-1})	0.268 (0.034)	1.307	1.223–1.398	7.85	< 0.001
Moisture index	−0.015 (0.003)	0.985	0.980–0.990	−5.52	< 0.001

Negative-binomial models fitted separately to account for over-dispersed recruitment counts (dispersion: spruce$_{)}$ = 1.68, pine$_{)}$ = 4.12). Rate ratios > 1 denote positive effects on recruitment.

Intensified storm activity has created canopy gaps through windthrow, as also reported in other studies (Gregow et al., 2017; Nilsson et al., 2004). Following the 2018 drought (Peters et al., 2020), *Ips typographus* outbreaks have further enhanced gap formation as colonised spruce die and fall (cf. Netherer et al., 2024). These combined disturbance processes maintain structural heterogeneity and improve light conditions for shade-intolerant species, even at this small spatial scale. Whether these disturbances facilitate pine recruitment remains to be seen.

4.3. Conservation implications for European forest reserves

In our reserve, strict protection coincided with structural recovery and a shift towards shade-tolerant *Picea abies*; this should not be read as a general expectation for European forest reserves. Small reserves face fundamental constraints: landscape-scale disturbance processes such as fire cannot fully manifest at their natural spatial scales. The more robust solution is reserve expansion to scales where natural disturbance regimes operate without constraint. Where expansion is not feasible, targeted measures that mimic the frequency and spatial grain of natural disturbance (e.g., low-intensity prescribed burns or creation of natural-sized gaps) can help maintain light-demanding biodiversity (Granström, 2001; Gustafsson et al., 2020; Hjältén et al., 2023). These should be explicitly framed as surrogates for missing large-scale disturbance processes that cannot manifest at their natural scales in small, isolated reserves. In contrast, at larger spatial scales, non-intervention remains the primary strategy, because natural disturbance regimes can operate and generate heterogeneity without active measures (Janda et al., 2017; Kuuluvainen and Aakala, 2011; Seidl et al., 2017). We believe that non-intervention and targeted management are scale-complementary rather than opposing doctrines: non-intervention is foundational at landscape scales, while in small, isolated reserves, minimal, process-mimicking actions can complement strict protection by approximating processes that cannot manifest at their natural scales (Bennett et al., 2009).

CRediT authorship contribution statement

Markus Franzén: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Emil Ideskär:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Victor Johansson:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Per Milberg:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation.

Declaration of competing interest

The authors declare no competing financial or personal interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111588.

Data availability

The data and R scripts are provided as supplementary files and will be deposited in Dryad upon acceptance

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