



Regeneration dynamics in response to an openness gradient caused by ash dieback, drought effects and understorey forest management in a meliorated European floodplain forest

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ARTICLE INFO

Keywords:

Regeneration
Forest management
Floodplain forest
Tree mortality
Canopy gaps
Forest disturbance
Drought stress
Growth response
Light gradient

ABSTRACT

Pathogens and droughts lead to increasingly thinned forests worldwide, shaping regeneration conditions. In Leipzig (Germany), we investigated the current structural change and regeneration responses in a meliorated floodplain forest, which is severely affected by recent drought events and ash dieback. Due to a lack of flooding, the spreading, flood-sensitive species *Acer pseudoplatanus*, *Acer platanoides* and *Sambucus nigra* darken the understorey. To promote light-demanding regeneration of *Quercus robur*, we combined natural canopy mortality with localised small-scale thinning in the understorey of the named spreading species. In this study, we examined the height and radial growth as well as vitality of the eight most common naturally regenerating tree species along this experimental openness gradient, across sites differing in overstorey vitality, with and without understorey thinning, between 2022 and 2023. Increased openness consistently promoted regeneration, but species differed markedly in their growth and vitality responses. The dominant *A. pseudoplatanus* exhibited strong height growth in response to openness across tree sizes but reduced vitality during drought, while *A. platanoides* maintained stable vitality and showed enhanced growth mainly in larger saplings. *Fraxinus excelsior* was strongly affected by disease, while *Tilia* spp. and *C. betulus* maintained high vitality even during drought, albeit, like *Ulmus* spp., with more radially oriented growth than the maples. Overall, the canopy openings currently enhance the dominance of already present, competitive species. We demonstrate that targeted small-scale understorey thinning can counteract this trend by supporting the growth of a diverse natural regeneration.

1. Introduction

Forests worldwide are currently undergoing major structural changes due to high tree mortality driven by climate change-related stressors, such as drought and pest outbreaks (Senf et al., 2020; Thonfeld et al., 2022). In Central European floodplain forests, this usually affects ecosystems that are already severely altered by hydrological regulations suppressing natural flooding dynamics and promoting homogeneous, shaded stands that limit the regeneration of light-demanding species such as pedunculate oak (*Quercus robur* L.; Härdtle et al., 2020; Henkel et al., 2025; Kopec et al., 2014; Mikulová et al., 2020). Today, the widespread canopy dieback is once again reshaping the structural and competitive environment of these forests, opening new regeneration niches and management opportunities for light-demanding tree species (Brunet et al., 2014; Lenk

et al., 2025). Understanding regeneration dynamics under these novel conditions is essential for predicting future forest composition, function, and resilience under ongoing climate change. Therefore, this study examines how canopy openings resulting from drought and ash dieback, partly combined with an experimental understorey thinning, affect the species composition, growth, and vitality of natural regeneration in a meliorated floodplain forest in Leipzig, Germany.

Today's regeneration layer determines the future of the forest, with regeneration success largely governed by stress tolerance and the ability to exploit limited resources (Goldberg, 1990; Grime, 1977; Pacala et al., 1996). In temperate forests, light is often the most contested resource (Balandier et al., 2008; Petriřan et al., 2009). Its spatio-temporal heterogeneity, driven by canopy structure and gap dynamics, determines seedling performance and growth strategies, leading to

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<https://doi.org/10.1016/j.foreco.2026.123791>

Received 16 January 2026; Received in revised form 2 April 2026; Accepted 6 April 2026

Available online 17 April 2026

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intra- and interspecific competition (Annighöfer et al., 2017; Walters and Reich, 1996). More light-demanding species typically attempt to escape shading through stronger height growth and respond to increased sunlight in gaps with rapid above-ground growth to reach the canopy more quickly. In contrast, shade-tolerant species typically invest more evenly in stem thickening, height, and root growth, allowing them to persist under lower light availability (Bebre et al., 2021; Petriřan et al., 2009). Such species differences in filling regeneration niches along resource gradients form the basis of species coexistence and, with that, biological diversity (Grubb, 1977; Pacala and Tilman, 1994).

Temperate floodplain forests are particularly heterogeneous ecosystems due to recurrent flooding, which generates mosaics of habitats differing in abiotic conditions, including soil moisture, sediment deposition and light availability (Havrdová et al., 2023; Schnitzler, 1994). Open canopies of characteristic species such as pedunculate oak and common ash (*Fraxinus excelsior* L.) enhance light penetration, promoting vertical structural complexity (Emborg, 1998). Together, spatial heterogeneity and temporal flood dynamics promote exceptionally high species richness (Havrdová et al., 2023; Tockner and Stanford, 2002; Ward et al., 1999). However, river regulation and groundwater lowering have fundamentally altered floodplain hydrology, creating more homogeneous, shaded forests in which generalist, flood-intolerant species such as sycamore (*Acer pseudoplatanus* L.) and Norway maple (*Acer platanoides* L.) often dominate (Engelmann et al., 2019; Härdtle et al., 2020; Hein et al., 2009). Their dense, shade-tolerant canopies further reduce understorey light and impede regeneration of characteristic light-demanding species such as pedunculate oak, a keystone species for biodiversity (Eaton et al., 2016).

Recently, pathogen outbreaks and recurrent droughts have opened canopies across European forests (Gazol and Camarero, 2022; George et al., 2022; Senf et al., 2020; Thonfeld et al., 2022), which can substantially alter understorey conditions (Alkama and Cescatti, 2016; Lembrechts and Nijs, 2020; Zellweger et al., 2020). Although floodplain forests are generally moist ecosystems, altered hydrological regimes and lowered groundwater tables expose trees to physiological stress, increasing their vulnerability (Henkel et al., 2025; Skiadaresis et al., 2019; Skovsgaard et al., 2017; Stojanović et al., 2015). Under these preconditions, novel extreme droughts associated with ongoing climate change may cause recurring disturbances resulting from drought-related mortality (Altman et al., 2024; Forzieri et al., 2021; Seidl et al., 2017). This raises the question of how interactions between hydrological alteration and climate change alter regeneration dynamics and influence the long-term persistence of characteristic floodplain forest biodiversity.

In our study area, the Leipzig floodplain forest, natural regeneration of the light-demanding pedunculate oak is strongly limited within in a system currently shaped by the convergence of several disturbance and stress factors, including altered hydrology, severe drought damage, and aggressive tree diseases such as ash dieback, sooty bark disease and Dutch elm disease (Henkel et al., 2025; Wirth et al., 2021). As a long-established silvicultural response to oak decline, oaks have been planted on small silvicultural cuttings ('femels') to ensure sufficient light. In this context, we set up an experiment in which we combined the current tree mortality-induced canopy gaps with small-scale management interventions (Lenk et al., 2025). Within 16×16 m subplots located in forest sites with either high (*mortality+*) or low (*mortality-*) overstorey tree mortality, the flood-intolerant, spreading tree species sycamore maple, Norway maple and elder (*Sambucus nigra* L.) were selectively removed from the understorey.

Canopy openings not only increase understorey light but also reduce the buffering of abiotic and biotic external influences, leading to changes in microclimate, nutrient inputs and organism pathways (Abd Latif and Blackburn, 2010; Frey et al., 2016; Perry et al., 2021; Verheyen et al., 2012; but see our study Lenk et al., 2024). Gap effects can coincide with additional climate-change impacts, such as extreme droughts, creating completely novel regeneration environments (De Frenne, 2024; Thom et al., 2023). This may disrupt established trade-offs between

growth and survival along light gradients and increase the importance of species-specific drought sensitivity for regeneration success and vitality (Fuchs et al., 2020; McGregor et al., 2021). For instance, water stress may constrain height growth and counteract light-driven growth strategies, while species adapted to shaded, stable microclimates may experience physiologically severe heat stress (Kunert and Hajek, 2022; Valladares and Niinemets, 2008). Beyond novel environmental conditions and species-specific traits, regeneration outcomes further depend on the size structure of the understorey, and established shade-tolerant advance regeneration may outcompete new seedlings when light increases (Lödige et al., 2014; Poorter et al., 2012). Consequently, canopy gaps may either enhance diversity by creating niches for light-demanding species or accelerate shifts towards communities dominated by a few competitive species (Collet et al., 2008; Hammond et al., 2021; Kwit and Platt, 2003). Such interacting factors make regeneration trajectories challenging to predict under ongoing environmental change.

In this study, we present an observational experiment that focuses on natural regeneration in the meliorated floodplain forest of Leipzig, affected by varying levels of overstorey mortality and by the presence or absence of an oak-oriented understorey management (*thinned* vs. *control* understorey). We aim to improve understanding of how this ecosystem responds to combined stresses from altered hydrology, climate change, and pathogen spread, informing management strategies to conserve biodiversity and resilience. Our analyses examine the response of regeneration to changes in structural stand characteristics, focusing on species composition and, for the most common tree species in the regeneration layer, on annual growth rates and vitality during the drought year of 2022 and the climatically more moderate year of 2023. In this context, we ask whether the management measure designed to sustain light restoration to promote planted oaks, while simultaneously reshaping the competitive environment of the naturally developing regeneration, also supports other typical tree species of the floodplain. We hypothesise (1) that sites with higher canopy mortality represent a more advanced stage of an openness-driven regeneration process, characterised by denser regeneration layers and reinforced dominance of already abundant species. (2) Annual growth (height and radial increment) is expected to increase with canopy openness across species, with stronger height responses in light-demanding species and comparatively greater radial allocation in shade-tolerant species. We hypothesise (3) that sapling vitality improves with canopy openness across all species in both years, with stronger positive effects in less shade-tolerant species. Vitality is expected to be reduced in the drought year 2022, though less pronounced in more drought-tolerant species.

2. Methods & material

2.1. Study site

The Leipzig floodplain in central Germany covers an area of approximately 5900 ha, of which around 33% is forest, one of the largest floodplain forests in Central Europe (Gläser, 2005). It is located within the climatic transition from maritime to continental conditions. Summers are warm, the mean annual temperature is 9.8°C , and average annual precipitation reaches 525 mm (DWD station Leipzig/Halle, 2024; annual mean temperature and precipitation sum for 1984 - 2023). The floodplain developed under the influence of the river system of Weiße Elster, Pleiße, Parthe and their tributaries. Periodic inundations shaped the hydrology, soil and vegetation. The accumulation of sediment following extensive historical deforestation had led to the soil formation of fertile loamy vega (Haase and Gläser, 2009). Under these conditions, a species-rich hardwood floodplain forest (*Ficario verna*-*Ulm*etum *campestris* KNAPP ex MEDWECKA-KORNAŚ 1952) developed, dominated by pedunculate oak (*Quercus robur* L.), common ash (*Fraxinus excelsior* L.), and elm species (*Ulmus minor* ALL., *U. laevis* PALL., *U. glabra* HUDS.). Today, the floodplain is largely protected by

the Natura 2000 directive, including four nature reserves, a landscape conservation area, and an EU Birds Directive Special Protection Area (Härdt et al., 2020; Prof. Hellriegel Institute, 2012). However, profound changes in the canopy composition have occurred over the past 150 years (Wirth et al., 2021; Gläser, 2005). The abandonment of the traditional forestry method, coppicing with oaks as standards, at the end of the 19th century reduced oak dominance while at the same time the cultivation and spread of common ash was promoted. In the mid-20th century, Dutch elm disease, caused by *Ophiostoma ulmi* (Buisman) NANNF and later the more aggressive *O. novo-ulmi* BRASIER, transmitted mainly by *Scolytus* GEOFFROY beetles, decimated elm populations in the overstorey. Today, the wind-dispersed pathogens *Hymenoscyphus fraxineus* (T. KOWALSKI) BARAL, QUELOZ, HOSoya, which cause ash dieback, and *Cryptostroma corticale* ELLIS & EVERH, which cause sooty bark disease, severely affect ash and maple populations. These biotic stresses are exacerbated by climatic extremes: following the drought years of 2018–2020, inventories revealed a lack of healthy, mature ash trees and widespread crown damage in various tree species (Henkel et al., 2025; Wirth et al., 2021). Furthermore, strong hydrological regulation through river dyking and straightening has suppressed the natural flooding regime and lowered the groundwater table, which was further enhanced through brown coal mining in the surrounding region (Gläser, 2005). In particular, the construction of the ‘Neue Luppe’ canal, which began in the 1930s, has been draining water from the floodplain since then. Only extreme events such as the floods of 1954, 2011, and 2013 have inundated large parts of the forest (LFULG, 2015). The loss of regular flooding has promoted flood-intolerant species such as sycamore (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), and elder (*Sambucus nigra* L.; Gläser, 2005). To preserve the proportion of light-demanding tree species typical of a hardwood floodplain forest, foresters carry out a management with so-called felmel cuttings. On these open, in the first years fenced, areas < 1 ha, with a few preserved habitat trees, tree species as pedunculate oak are planted.

2.2. Experimental design

In our research project, we have implemented a new management approach to promote the regeneration of light-demanding tree species, especially *Q. robur*, that incorporates the new canopy openings caused by drought and diseases (Lenk et al., 2024, 2025). Between December 2021 and February 2022, we established sixteen research plots (0.25 ha each). Eight plots were located in forest stands with largely intact overstorey (*mortality*-), while eight plots were situated in stands strongly affected by recent overstorey decline, primarily caused by ash dieback and sooty bark disease (*mortality*+). Half of the plots per vitality status were placed in the northern floodplain, the other half in the southern floodplain (Fig. 1). Each plot was subdivided into four 25 × 25 m quadrants, each containing one 8 × 8 m subplot. In addition to the naturally occurring variation in canopy openness resulting from differences in overstorey vitality, a targeted silvicultural intervention was applied at the subplot level. This treatment consisted of selectively removing trees with a diameter at breast height < 20 cm of the flood-sensitive species *A. pseudoplatanus*, *A. platanoides*, and *S. nigra* in winter 2022 and repeated in winter 2023 to remove resprouts and newly emerged seedlings. The thinning was carried out on an area of 16 × 16 m centred on every second subplot. All cut material was retained on site. This intervention aimed towards a tree species composition typical of hardwood floodplain forests, characterised by tolerance to short-term flooding. It is important to note, however, that this method does not address important key aspects of flooding, such as sediment accumulation, erosion, nutrient or acorn transport, or increased soil moisture (Gregory et al., 1991; Havrdová et al., 2023). Subplots that did not receive the *thinning* treatment were maintained as *controls*. In a first study, we investigated microclimate and biological soil activity in this experimental setup (Lenk et al., 2024); in a second study, we examined the development of planted oak seedlings (Lenk et al., 2025). In the present study, we analyse the development of natural tree regeneration, with a focus on growth and vitality of the eight most frequently occurring species: *Acer pseudoplatanus* L., *Acer platanoides* L., *Sambucus nigra*

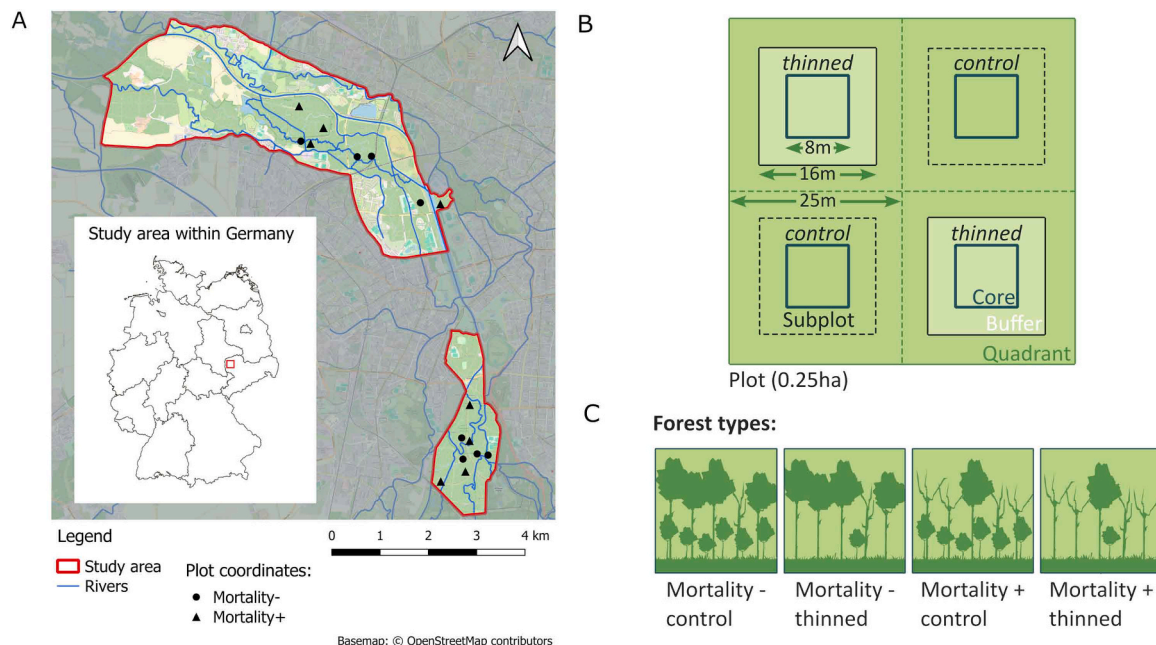


Fig. 1. Map and experimental design defining four different forest types modified after Lenk et al. (2024), (2025). (A) Map of the study area in the Leipzig floodplain forest with the 16 research plots, eight plots each in forest with high mortality in the overstorey (*mortality*+) and low mortality in the overstorey (*mortality*-). (B) Each forest plot, 0.25 ha in size, comprises four 25 × 25 m quadrants, with an 8 × 8 m subplot. On and around the *thinned* subplots 16 × 16 m, trees with a smaller diameter at breast height than 20 cm of *Acer pseudoplatanus*, *A. platanoides*, and *Sambucus nigra* were cut in winter 2022. Resprouts, as well as new germinated seedlings, were again removed in the following winter of 2023. *Control* subplots stayed untreated. (C) This design results in four categories, referred to as forest types: *mortality*- *control*, *mortality*- *thinned*, *mortality*+ *control* and *mortality*+ *thinned*.

L., *Tilia cordata* MILL., *Tilia platyphyllos* SCOP., *Ulmus* spp. (*U. minor* ALL., *U. laevis* PALL., *U. glabra* HUDS. and hybrids), *Fraxinus excelsior* L. and *Carpinus betulus* L. We pooled the elms at the genus level, as distinctive characteristics are often not yet recognisable in the regeneration stage, and the species hybridise strongly with each other.

To assess differences in over- and understorey canopy openness within the four forest types (*mortality-thinned*, *mortality-control*, *mortality+thinned*, *mortality+control*), hemispherical photographs were taken at the centre of each subplot in July 2022 and 2023. Images were recorded at heights of 0.9 m and 5 m using a digital camera equipped with a fisheye lens (Nikon Coolpix P5100 with Nikon FC-E20 fisheye converter, Japan). Canopy openness was derived from the photographs by classifying individual pixels as either sky or canopy based on RGB colour values, using the WinSCANOPY Pro 2009a software (Regent Instruments Inc., Canada).

2.3. Tree inventory

2.3.1. Canopy

In summer 2022, we conducted an inventory of all trees across the entire research plots, recording each stem with a diameter at breast height (DBH) ≥ 5 cm separately and tagging it with a unique ID. For each stem, species identity, vitality, damage and DBH, measured at 1.30 m height to the nearest 0.5 cm using a diameter tape, were recorded. Species composition was calculated based on the basal area (m²) per tree:

$$\text{basal area} = \pi * \frac{(\text{DBH} \div 2)^2}{10000} \quad (1)$$

We classified tree vitality in categories as ‘vital’, ‘normal’, ‘puny’, or ‘dead’. Trees assigned to the ‘vital’ category were not only in good health but also stood out by their dominance, expressed in exceptional crown development and spatial prominence within the stand. Visible damage - including injuries, stem or crown breakage, crown thinning (e.g. due to drought), rot, and bark peeling - was assessed and scored for severity (1 = slight, 3 = severe). Trees that had one or more damages with a severity of at least 2 were categorised as ‘puny’. When grouping plots by vitality categories derived from our inventory, the ranking does not perfectly match the predefined mortality classes of the experimental setup (Fig. S1). This deviation can be explained by the time lag between plot establishment in winter 2021/2022 and the first inventory in summer 2022, and particularly by the fact that already downed deadwood was not included in the inventory.

In addition, we evaluated ash dieback using the five-class system of Langer et al. (2015), ranging from class 1 (slightly damaged trees with minor crown foliage loss) to class 5 (dead or dying trees with crown loss, emergency shoots on the trunk, severe bark beetle infestation, and wood decay at trunk base and roots). The occurrence of sooty bark disease was assessed in three classes: class 1 (crown with slightly reduced foliage, some shoot tips without leaves, dead branches in the crown area), class 2 (crown with significantly reduced foliage, numerous shoot tips without leaves, dead branches in the crown area, fruiting bodies of *C. corticale* on strong branches), and class 3 (dead or dying trees, crown almost completely defoliated, emergency shoots on the trunk or strong branches, fruiting bodies of *C. corticale* on strong branches and on the trunk).

In summer 2023, the vitality assessment and disease monitoring were repeated for trees with DBH ≥ 20 cm to evaluate temporal trends in overstorey condition. In the following, trees with DBH ≥ 20 cm are referred to as overstorey trees, and trees with DBH ≥ 5 cm as canopy trees.

2.4. Regeneration

In both summers 2022 and 2023, the regeneration layer, defined as all trees with a height ≥ 50 cm and DBH < 5 cm, was inventoried on the

8 × 8 m subplots. Trees were marked with a unique aluminium ID tag and recorded individually for height, root neck diameter, vitality, and damage. For multi-stem trees, we recorded every stem with at least 50 cm height separately.

Tree height was measured from the ground vertically to the highest shoot tip with a 2 m folding rule to the nearest 0.5 cm, without straightening the tree. Taller trees were measured using a Vertex Laser Geo 360° device (Haglöf Sweden AB, Långsele, Sweden). Root neck diameter was measured directly above the ground with an electronic calliper (Kunzer 7EMS02, Willy Kunzer GmbH, Munich, Germany) to the nearest 0.01 mm.

We classified tree vitality as either ‘normal’ or ‘puny’, excluding dead trees from the inventory. Since trees in this layer did not exert dominance within the stand and encompassed a wide range of age classes, we did not apply a ‘vital’ category, as used in the canopy or in our monitoring of planted oaks (Lenk et al., 2025). If a tree were strongly damaged or was not well developed, it was classified as ‘puny’. Insect damage, browsing, drought damage and other damage (e.g., broken stems, leaf fungi, etc., which were noted as a comment) were scored from 1 (slight) to 3 (severe).

Vegetation density was estimated per species and subplot. Root neck diameter was converted to basal area (m²) using the circular area formula (see Formula 1), with a conversion factor of 10⁶ to transform mm² to m².

All trees from the first-year inventory were re-inventoried in the second year, regardless of whether DBH exceeded 5 cm. Trees reaching at least 50 cm in height for the first time were additionally included. Annual relative height and radial growth rates were calculated from the 2022–2023 measurements for each tree:

$$\text{relative growth rate} = \frac{\ln(\text{size}_2) - \ln(\text{size}_1)}{t_2 - t_1} \quad (2)$$

where *size*₁ and *size*₂ are the measured heights or root neck diameters in 2022 (*t*₁) and 2023 (*t*₂), respectively (Hunt et al., 2002). The absolute growth rates resulted from the differences between the measurements from 2023 and 2022.

In general, all trees in the regeneration layer of a subplot were recorded individually. However, sycamore and Norway maple sometimes covered > 50% of a subplot. In these cases, inventories were conducted along 50 cm-wide transects (two orthogonal lines crossing the subplot centre from the middle of the subplot boundaries, 25 cm on each side). Basal areas obtained from these transects (7.75 m², 12.1% of the subplot) were extrapolated to the full 64 m² subplot. Trees ≥ 5 m in height were not extrapolated and were included in the inventory regardless of their location inside or outside the transect; their basal area was added to the extrapolated subplot total.

2.5. Data analysis

All analyses were conducted in R version 4.4.0 (R Core Team, 2024).

We described the species composition of the canopy and regeneration layers based on the proportional basal area of tree species in 2022. For the regeneration layer, only data from unmanaged *control* subplots were used, while in the canopy layer, trees with a DBH < 20 cm were excluded from *thinned* subplots and their buffer zones to avoid bias, as *A. pseudoplatanus*, *A. platanoides* and *S. nigra* had been selectively removed there. To assess variability among plots, we calculated the coefficient of variation of basal area per species and used Levene’s tests to assess differences in the variance of basal area among species across plots. To analyse differences in basal area sums per plot between species and vitality status in the canopy (2022), we applied two linear mixed-effects models with block (northern vs. southern floodplain) as a random intercept, one including and one excluding standing dead wood. For the regeneration layer, we used the recorded sum of basal areas in 2022 and 2023 per subplots and extended the model by including year

as an interacting predictor. Subplot ID nested within plot ID nested within block ID was specified as a random intercept to reflect the hierarchical study design.

To assess the influence of forest type (categorical) or canopy openness (continuous) together with tree species identity and initial tree height on the growth and vitality of the regeneration of the eight most common tree species, we fitted further mixed-effects models. These models followed the same random-effects structure as described above for the regeneration layer. Growth responses (absolute and relative height growth, absolute and relative radial growth) were analysed with linear mixed-effects models (lme4; Bates et al., 2015). For tree vitality, as a binary response (normal or puny vitality), we opted for generalised linear mixed-effects models using a binomial error distribution (glmmTMB; Brooks et al., 2017) and included only data with at least three trees of a species per subplot and year.

For the growth analysis, we used the mean openness from 2022 and 2023, whereas for the vitality models, the year-specific openness values were applied. Each tree was assigned a canopy openness value based on measurements at two standard heights at the centre of each subplot (0.9 m and 5 m). For trees with heights between these points, values were linearly interpolated, while trees shorter than 0.9 m or taller than 5 m were assigned the value of the nearest measured height to avoid extrapolation. Trees with broken stems, bitten-off main axes, or strongly deformed growth forms (e.g. suppressed by deadwood) were excluded from growth analyses.

Tree height was log-transformed to reduce the skewness of the data distribution with a surplus of small trees. All continuous predictors were z-transformed before modelling; for visualisation, results were back-transformed to the original scale.

To test the influence of forest type (categorical), we ran two separate model sets based on different data frames. In the first, we compared all forest types but excluded *A. pseudoplatanus*, *A. platanoides* and *S. nigra*, since these species were removed from the *thinned* subplots. In the second, we retained all species but restricted the analysis to the *control* subplots, thereby comparing the vitality status of the forest canopy without excluding species. The full models included as fixed effects forest type, tree species, log-transformed initial tree height, and the two-way interactions with forest type and tree height, as well as species and tree height. For the vitality models, year was added as an additional predictor, including its interactions with species, tree height and forest type. Due to sparse data for some combinations, interactions between forest type and species were not modelled.

Instead, in the models with openness (continuous) assigned to every single tree, the full data set could be analysed at once. These models contained the same set of predictors as the forest type models, but with openness replacing forest type. Analyses were conducted once across all subplots (*control* and *thinned*) to capture the full openness gradient, and once restricted to *control* subplots to represent natural canopy conditions and species pools. In addition to the across-species models, we fitted species-specific models to account for substantial differences in the observed ranges of initial tree height and canopy openness among species (Table S1). While the across-species models highlighted differences between species, the species-specific models allowed us to assess effects within the observed values for each species. For these models, we refitted the same set of predictors (openness, tree height, and, for vitality, also year) per species. For the full models, we included all interaction terms supported by data availability. In the growth models, this comprised all possible interactions. In the vitality models, the across-species full model included all possible two-way interactions but no higher-order terms, while the species-specific models included all interaction terms except for *C. betulus* and *T. platyphyllos*, for which we fitted purely additive models due to sparse and unbalanced data. For some species-specific models, we reduced the random-effects structure when required to achieve model convergence and stability. Details for each model are provided in the respective result tables.

For all models concerning the growth and vitality of the regeneration

and resprouts, we performed model selection on the interaction terms. All main effects were retained in every model, i.e. purely additive models were the simplest model version. Competing models were compared using the sample-size corrected Akaike Information Criterion (AICc) to identify the best-supported model (Burnham and Anderson, 2002). Among all models within 2 Δ AICc of the top-ranked model, we selected the simplest model, following the principle of parsimony (Arnold, 2010; Bird et al., 2020). In the results section, we either report all retained fixed effects (main effects and the selected interaction terms) of the final models in the text and/or refer to the supplement.

Model assumptions were assessed visually for linear models using the ‘performance’ package (Lüdtke et al., 2021), whereas for binomial models, simulated residuals were examined with the ‘DHARMA’ package (Hartig, 2024). In linear models, fixed effects were tested with *t*-tests using Satterthwaite approximation (‘lmerTest’; Kuznetsova et al., 2017), and random effects were assessed with restricted likelihood ratio tests. Predictor significance was assessed using F-tests implemented via the ‘anova’ function. For the generalised models, fixed effects were tested using z-tests based on maximum likelihood estimation, and Wald χ^2 tests were conducted using the ‘Anova.glmmTMB’ function. For all models, *post-hoc* comparisons were performed with the ‘emmeans’ package (Lenth, 2025), applying Tukey-adjusted contrasts for both pairwise differences of estimated marginal means and slope comparisons via the ‘emtrends’ function. Statistical significance is reported as $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

3. Results

3.1. Species composition and structural stand characteristics

Among canopy trees (DBH ≥ 5 cm), *Q. robur* accounted for the largest share of basal area (Fig. 2, Table S2). Its distribution across plots was heterogeneous, as reflected by a coefficient of variation (CV) of 112%. The diameter distribution showed that the largest trees in the study region were oaks and that small oaks were strongly underrepresented (Fig. 3, Fig. S2). *Quercus robur* was almost absent in the regeneration layer, with only one tree, 50 cm tall, found on a *control* subplot (Fig. 2, Tables S2 and S3). In contrast, the regeneration layer was dominated by young maples, particularly *A. pseudoplatanus*, followed by *A. platanoides*. Together, the basal areas of these two species accounted for 63.9% of the regeneration layer, compared to 21.9% of the canopy (Fig. 2). Within the canopy, numerous maple trees were concentrated in the smaller diameter classes, with more large individuals in *A. pseudoplatanus* than *A. platanoides* (Fig. 3, Fig. S2). *Acer pseudoplatanus* showed a relatively even distribution across plots in both canopy (CV = 69.3%) and regeneration (CV = 69.5%), whereas *A. platanoides* exhibited a more heterogeneous pattern, particularly in the regeneration layer (regeneration CV = 156%; canopy CV = 83.5%). In 2022, 22.3% of *A. pseudoplatanus* individuals in the canopy and 38.9% in the overstorey (DBH ≥ 20 cm) showed symptoms of sooty bark disease, whereas *A. platanoides* was hardly affected (Fig. S3). The third native maple species, *A. campestre*, occurred at low frequencies in both the canopy and the regeneration layer (Fig. 2). Living *F. excelsior* trees were still frequent in the canopy (Fig. 2), but most showed severe ash dieback symptoms. Including standing deadwood, 92.3% of the trees inventoried were infected, and 89.2% when considering only living individuals. All overstorey trees with DBH ≥ 20 cm showed symptoms (Fig. S4). Canopy trees of *F. excelsior* were evenly distributed across plots (CV = 70.7%), whereas the regeneration layer was highly clustered (CV = 270%). In the regeneration layer, *F. excelsior* occurred at similar frequencies as *Tilia* spp. and *Ulmus* spp. Among the two lime species, *T. platyphyllos* was less common and more unevenly distributed in the canopy (CV = 187%) than *T. cordata* (CV = 96.5%, Levene’s test: $F_{1,30} = 9.68$, $p < 0.01$), although their frequencies and intermediately clustered spatial distribution in the regeneration layer were similar (*T. platyphyllos* CV = 188%, *T. cordata* CV = 167%, Levene’s test: $F_{1,30} = 0.03$,

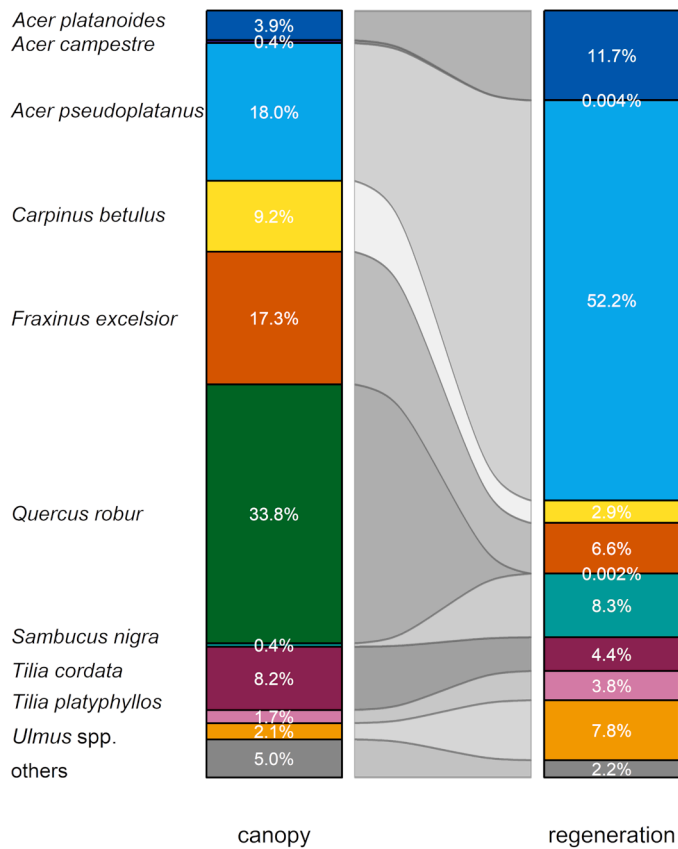


Fig. 2. Relative proportion of basal area of living trees per species in the canopy and regeneration layer in 2022. Canopy trees (DBH ≥ 5 cm) are included from the entire plot areas, exclusive trees with DBH < 20 cm on the *thinned* subplots and the buffer zone around them. For the regeneration layer, we included the data of the *control* subplots with trees at least 50 cm tall and a DBH < 5 cm. Elm species are grouped at the genus level. If a species occupied more than 50% of the subplot in the regeneration layer, an area-based transect method was used, and the basal areas were extrapolated to the entire subplot.

$p = 0.86$; all pairwise comparisons, see Table S4 for canopy and S5 for regeneration.). *Ulmus* spp. were much more locally concentrated in the regeneration (CV = 237%) and almost absent from the canopy due to Dutch elm disease, with the few remaining individuals scattered

(CV = 159%). Another common species in the canopy, *C. betulus*, showed intermediate variability across plots (CV = 125%). In the regeneration layer, it occurred locally in small clusters (CV = 234%), with a small overall contribution to the regeneration layer (Fig. 2, Table S2). *Sambucus nigra*, a shrubby species, was as frequent in the regeneration layer as *Tilia* spp., *Ulmus* spp., and *F. excelsior*, and showed an intermediate CV of 152%.

In addition to the species already mentioned, other woody species were recorded in low numbers during monitoring, including *Alnus glutinosa* (L.) GAERTN., *Aesculus hippocastanum* L., *Acer negundo* L., *Corylus avellana* L., *Crataegus laevigata* (POIR.) DC., *Crataegus monogyna* JACQ., *Euonymus europaeus* L., *Fagus sylvatica* L., *Fraxinus pennsylvanica* MARSHALL, *Malus sylvestris* L. (MILL.), *Prunus avium* (L.) L., *Prunus padus* L., *Prunus spinosa* L., *Quercus rubra* L. and *Taxus baccata* L. (Figs. S5 and S6). The species composition of the regeneration layer on the *thinned* subplots is shown in comparison to the *control* subplots in the appendix for both forest vitality categories (Table S3).

Canopy basal area per plot differed between forest vitality categories depending on species composition (only living trees: $F = 2.35$, $p < 0.05$; including standing dead wood: $F = 2.45$, $p < 0.05$), mainly due to higher *Q. robur* basal area on *mortality-* plots (Fig. S7). In 2022, 44.3% of overstorey trees were classified as puny or dead, ranging from 22.2% to 74.5% across plots (Fig. S1). Between 2022 and 2023, 30 overstorey trees (4.5%) died equally distributed across *mortality+* and *mortality-* plots (Figs. S5 and S8), mainly *F. excelsior* (14 out of 119 trees) and *A. pseudoplatanus* (9 out of 180 trees). Extremely vital and dominant trees with spreading crowns occurred predominantly on *mortality-* plots, and were mostly *C. betulus*.

The regeneration density (the sum of basal areas) per species and subplot was similar between *mortality-* and *mortality+* sites ($F = 0.06$, $p = 0.82$) and between years ($F = 0.15$, $p = 0.7$), whereas species identity showed a strong significant effect ($F = 36.08$, $p < 0.001$) with *A. pseudoplatanus* having a significantly higher sum of basal area than all other species. Furthermore, the interaction between forest vitality status and species identity was marginally significant ($F = 1.85$, $p = 0.07$) with the sum of basal area of *A. pseudoplatanus* being significantly higher on *mortality+* than on *mortality-* (Fig. S9). This was underlined by the diameter class distribution displaying a higher proportion of larger *A. pseudoplatanus* individuals in *mortality+* than in *mortality-* (Fig. S10). Although not significant in the model, perhaps due to generally low occurrence, the low tree counts of *C. betulus*, *Ulmus* spp. and *T. platyphyllos* on *mortality+* compared to *mortality-* were striking (Table S3, Fig. S10). Between 2022 and 2023, 652 trees in the regeneration

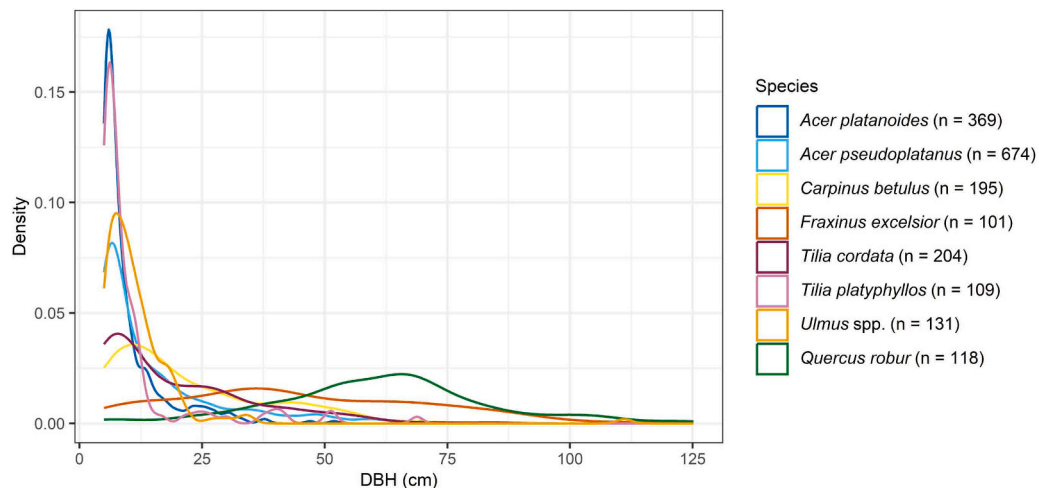


Fig. 3. Density distributions of diameter at breast height (DBH) in cm for canopy trees per species. Legend labels indicate sample size (n). All living trees with DBH ≥ 5 cm were included, except trees with DBH < 20 cm on *thinned* subplots and their buffer zones. Histograms showing absolute frequencies per DBH class are provided in Fig. S2 for the canopy and in Fig. S10 for the regeneration layer, assigned to the forest vitality categories *mortality+* and *mortality-*.

inventory either died or were not relocated during the second survey (Fig. S11), with *F. excelsior* experiencing the highest relative loss (98 of 719 trees, 13.6%; Fig. S6). For *F. excelsior*, no individuals with a root neck diameter larger than 34 mm were found in the regeneration layer, whereas all other species included individuals exceeding 60 mm (Fig. S10). In 2023, 817 further trees surpassed 50 cm in height, with *A. pseudoplatanus* accounting for the largest share with 672 new trees (Figs. S6 and S11).

3.2. Growth of the regeneration

3.2.1. Forest type effect

The forest type affected mainly radial tree growth, while the only significant effect of forest type on height growth occurred in interaction with initial tree height on absolute growth within the *control* forest dataset ($F = 8.21$, $p < 0.01$). Growth increased with initial tree height ($F = 39.47$, $p < 0.001$), and this relationship was significantly steeper at *mortality+* than at *mortality-* sites (see effect plot Fig. S12). Both relative and absolute height growth differed significantly among species in both data sets, with significant interactions between species and tree height (Tables S6 and S7).

Relative and absolute radial growth were significantly influenced by forest type in the dataset, including all forest types ($F_{\text{rel}} = 8.78$, $p_{\text{rel}} < 0.001$; $F_{\text{abs}} = 5.62$, $p_{\text{abs}} < 0.01$). *Mortality+ thinned* stands showed higher mean relative radial growth ($0.19 \pm 0.03 \text{ yr}^{-1}$) than other forest types. Similarly, absolute radial growth was greater in *mortality+ thinned* stands ($3.11 \pm 0.62 \text{ mm/yr}$), exceeding *mortality+ control* by $2.33 \pm 0.73 \text{ mm/yr}$ and *mortality- control* by $2.68 \pm 0.71 \text{ mm/yr}$. Moreover, the interaction between forest type and initial tree height significantly affected radial growth ($F_{\text{rel}} = 4.53$, $p_{\text{rel}} < 0.01$; $F_{\text{abs}} = 5.94$, $p_{\text{abs}} < 0.001$). While most forest types showed a weakly positive relationship between initial height and relative radial growth with confidence intervals spanning zero, *mortality+ thinned* sites displayed a negative relationship, significantly differing from all other forest types (Fig. S12). Absolute radial growth increased with initial tree height in most forest types, but showed no detectable effect in *mortality- control* sites. *Mortality- thinned* sites differed significantly from *mortality- control* sites (Fig. S12). Additionally, absolute and radial growth were influenced by the interaction between species identity and tree height (Table S6). Within the *control* forest subset of the data, this interaction remained a significant predictor for both radial growth measures, and

tree height alone also significantly predicted absolute radial growth (Table S7). Pairwise species comparisons are reported in the next subchapter on the openness model.

3.2.2. Openness gradient

To complement the forest type analysis, we examined growth responses along a continuous gradient of canopy openness. Across all growth measures, openness had a consistent positive effect on tree growth, while species identity explained substantial variation in the sensitivity to openness, particularly for height-related measures (Table 1 and S8). Absolute height and absolute radial growth were further predicted by initial tree height. Importantly, several interactions shaped the growth responses. A pervasive pattern across all four growth measures was the species-specific dependence on tree height. For absolute height and radial growth, this relationship further varied with openness, reflecting a significant three-way interaction among species, openness, and tree height. Species also differed in their responsiveness to openness, influencing both height growth measures and relative radial growth. Finally, the positive effect of openness on height growth weakened with increasing tree height, but this interaction was only significant for relative height growth.

Post-hoc comparisons based on estimated marginal means showed that *A. pseudoplatanus* generally exhibited the fastest height growth across species. It exceeded most other species in relative height growth (except *A. platanoides* and *T. platyphyllos*), whereas differences in absolute height growth were limited and mainly involved *Ulmus* spp. It also showed a stronger responsiveness to openness than *Ulmus* spp. in relative height growth and, for larger trees, in absolute height growth compared with *Ulmus* spp. and *T. cordata*. *Acer platanoides* showed a similar pattern relative to *Ulmus* spp., with higher relative height growth and a steeper openness response in absolute height growth of larger trees. Species differences in relative radial growth were not significant. However, in *S. nigra*, the positive openness effect on absolute radial growth shifted to negative with increasing tree size, contrasting significantly with the consistently positive responses observed in most other species. *Tilia cordata* showed a particularly strong positive openness response in radial growth for larger trees, significantly exceeding *F. excelsior*, *Ulmus* spp. and *C. betulus*. For an impression of species growth rates, see Fig. 4 (species-specific models); full *post-hoc* results from the across-species models are provided in Tables S9 - S12.

Across-species models revealed general patterns and differences

Table 1
Growth responses of tree regeneration to species identity, openness, and initial tree height.

Predictor	Num DF	SS	MS	F	p	SS	MS	F	p
					Relative height growth $R^2_{\text{m}} = 0.14$; $R^2_{\text{c}} = 0.27$				
species	7	1.13	0.16	9.82	***	1.8	0.26	3.8	***
openness	1	0.61	0.61	36.95	***	2.21	2.21	32.62	***
tree height	1	0.05	0.05	2.99	0.08	0.78	0.78	11.45	***
Species:openness	7	0.33	0.05	2.87	**	1.87	0.27	3.95	***
Species:tree_height	7	0.36	0.05	3.15	**	0.95	0.14	2.00	0.05
Openness:tree_height	1	0.13	0.13	7.72	**	0.01	0.01	0.18	0.67
Species:openness:tree_height	7	-	-	-	-	1.5	0.21	3.17	**
					Relative radial growth $R^2_{\text{m}} = 0.07$; $R^2_{\text{c}} = 0.15$				
species	7	0.12	0.02	0.9	0.51	21.32	3.05	0.5	0.83
openness	1	0.38	0.38	20.13	***	146.86	146.86	24.24	***
tree height	1	0.01	0.01	0.67	0.42	83.13	83.13	13.72	***
Species:openness	7	0.38	0.05	2.88	**	53.3	7.61	1.26	0.27
Species:tree_height	7	0.34	0.05	2.59	*	96.24	13.75	2.27	*
Openness:tree_height	1	-	-	-	-	9.03	9.03	1.49	0.22
Species:openness:tree_height	7	-	-	-	-	168.98	24.14	3.99	***
					Absolute height growth $R^2_{\text{m}} = 0.14$; $R^2_{\text{c}} = 0.25$				
species	7	1.13	0.16	9.82	***	1.8	0.26	3.8	***
openness	1	0.61	0.61	36.95	***	2.21	2.21	32.62	***
tree height	1	0.05	0.05	2.99	0.08	0.78	0.78	11.45	***
Species:openness	7	0.33	0.05	2.87	**	1.87	0.27	3.95	***
Species:tree_height	7	0.36	0.05	3.15	**	0.95	0.14	2.00	0.05
Openness:tree_height	1	0.13	0.13	7.72	**	0.01	0.01	0.18	0.67
Species:openness:tree_height	7	-	-	-	-	1.5	0.21	3.17	**
					Absolute radial growth $R^2_{\text{m}} = 0.14$; $R^2_{\text{c}} = 0.22$				
species	7	0.12	0.02	0.9	0.51	21.32	3.05	0.5	0.83
openness	1	0.38	0.38	20.13	***	146.86	146.86	24.24	***
tree height	1	0.01	0.01	0.67	0.42	83.13	83.13	13.72	***
Species:openness	7	0.38	0.05	2.88	**	53.3	7.61	1.26	0.27
Species:tree_height	7	0.34	0.05	2.59	*	96.24	13.75	2.27	*
Openness:tree_height	1	-	-	-	-	9.03	9.03	1.49	0.22
Species:openness:tree_height	7	-	-	-	-	168.98	24.14	3.99	***

Notes: Results of linear mixed-effects models predicting annual relative and absolute height and radial growth of regeneration. Fixed effects included species identity, openness, and log-transformed initial tree height, along with all two- and three-way interactions in the full model. Random effects accounted for the split-plot design, with subplot ID nested within plot ID and block ID. Model selection was based on AICc, with the simplest model chosen if it lay within 2 ΔAICc of the top-ranked model. The table reports ANOVA results with the numerator degrees of freedom (Num DF), sums of squares (SS), mean squares (MS), F-values, and p-values together with marginal and conditional R^2 for each model. Detailed model summaries are presented in Table S8.

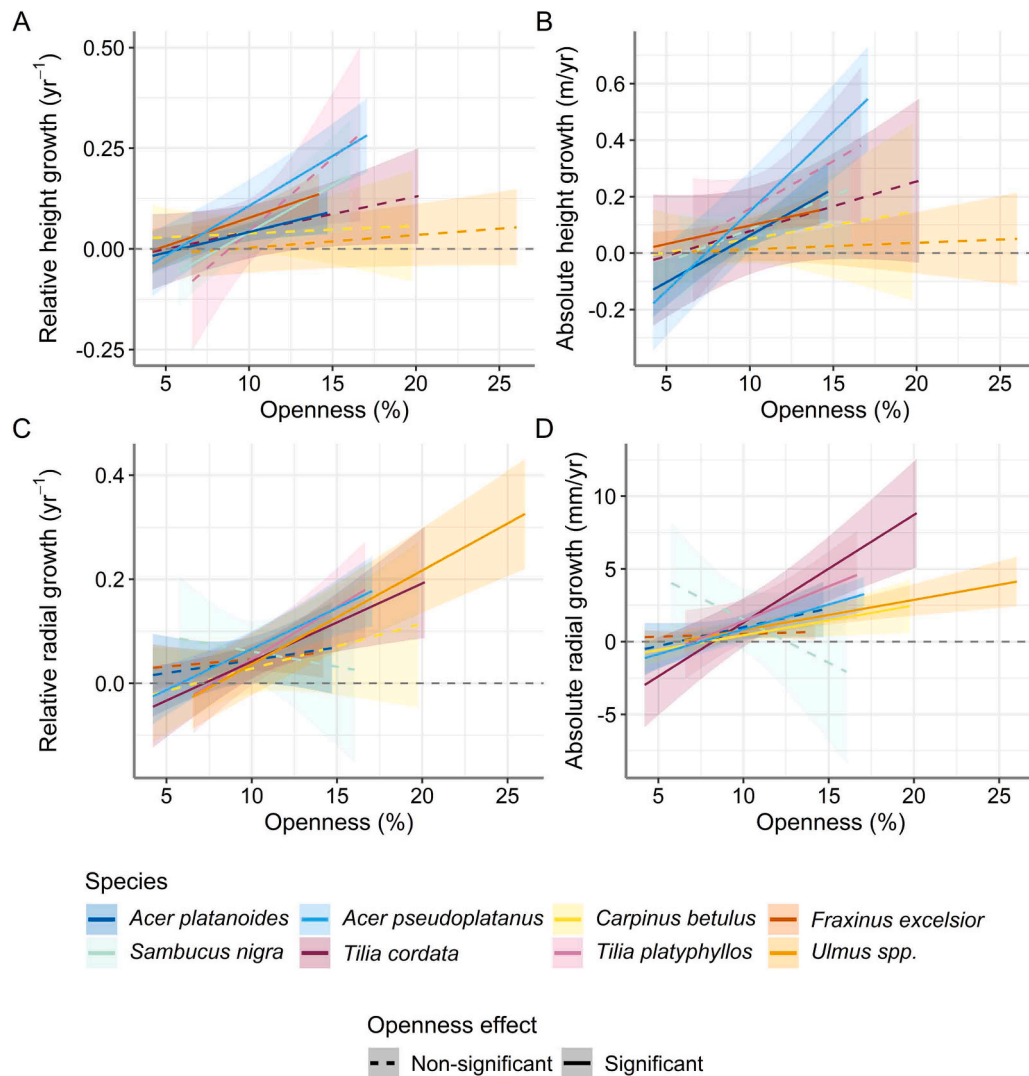


Fig. 4. Effect of openness on the growth of regeneration at mean height per species. For each growth response (relative height growth, absolute height growth, relative radial growth, absolute radial growth), the best parsimonious linear mixed-effects model was selected via AICc for each species using the predictors openness and log-transformed tree height, with or without an interaction term. Random intercepts were fitted with subplot ID nested within plot ID and block ID. In the relative height growth model of *C. betulus* block ID was eliminated from the random effect to achieve model convergence. Model summaries are reported in Table S13.

between species, but they mask the fact that species grew under markedly different initial tree sizes and light conditions. To account for these differences, we fitted separate models for each species within their observed ranges of tree height and openness, which varied substantially among species (e.g. 1.2–2.9 m in mean height, 8.1–11.0% in mean openness; Table S1). The following species-specific models thus illustrate how openness, initial tree height, and their interactions influenced growth within the realised ecological context of each species (Figs. 4 and 5).

For all species, openness effects were consistently positive, and tree height effects were generally positive for absolute growth but negative for relative growth when significant. All statistical results are summarised in Table S13. *Acer pseudoplatanus* followed this full pattern, showing significant positive openness effects for all measures (Fig. 4), positive height effects for absolute growth, negative height effects for relative growth, and a negative interaction for relative height growth (Fig. 5). *Acer platanoides* largely matched the general trend in height growth but uniquely exhibited significant positive openness–height interactions for all measures except relative height growth. *Fraxinus excelsior* responded significantly positively to openness in height growth and to tree height in absolute growth. Other species showed more isolated significant

effects: *Carpinus betulus* displayed a positive interaction on absolute height growth and a positive openness effect on absolute radial growth, whereas *S. nigra* had a positive openness effect on relative height growth with a negative interaction. *Tilia platyphyllos* showed a positive openness effect for radial growth and a negative height effect only for relative radial growth, while *T. cordata* had positive openness effects in both radial growth measures, but no significant effect for absolute height growth and a negative interaction effect of tree height and openness on relative height growth. *Ulmus spp.* exhibited positive openness effects for both radial growth measures, a positive height effect for absolute radial growth, and a negative height effect for relative height growth.

Analyses of the *control* dataset, which excludes managed subplots and thus reduces the openness gradient, generally confirmed the full-dataset results (Tables S14 – S16). Notably, in this dataset *T. platyphyllos* additionally responded to openness in height growth and showed negative height interactions affecting relative height growth as well as relative and absolute radial growth. Further deviations were limited: Openness effects disappeared for *Ulmus spp.* and *T. cordata* in relative radial growth and for *C. betulus* in absolute height growth. Moreover, a positive interaction of *F. excelsior* on absolute radial growth newly appeared, while the interaction effect of *C. betulus* on absolute height

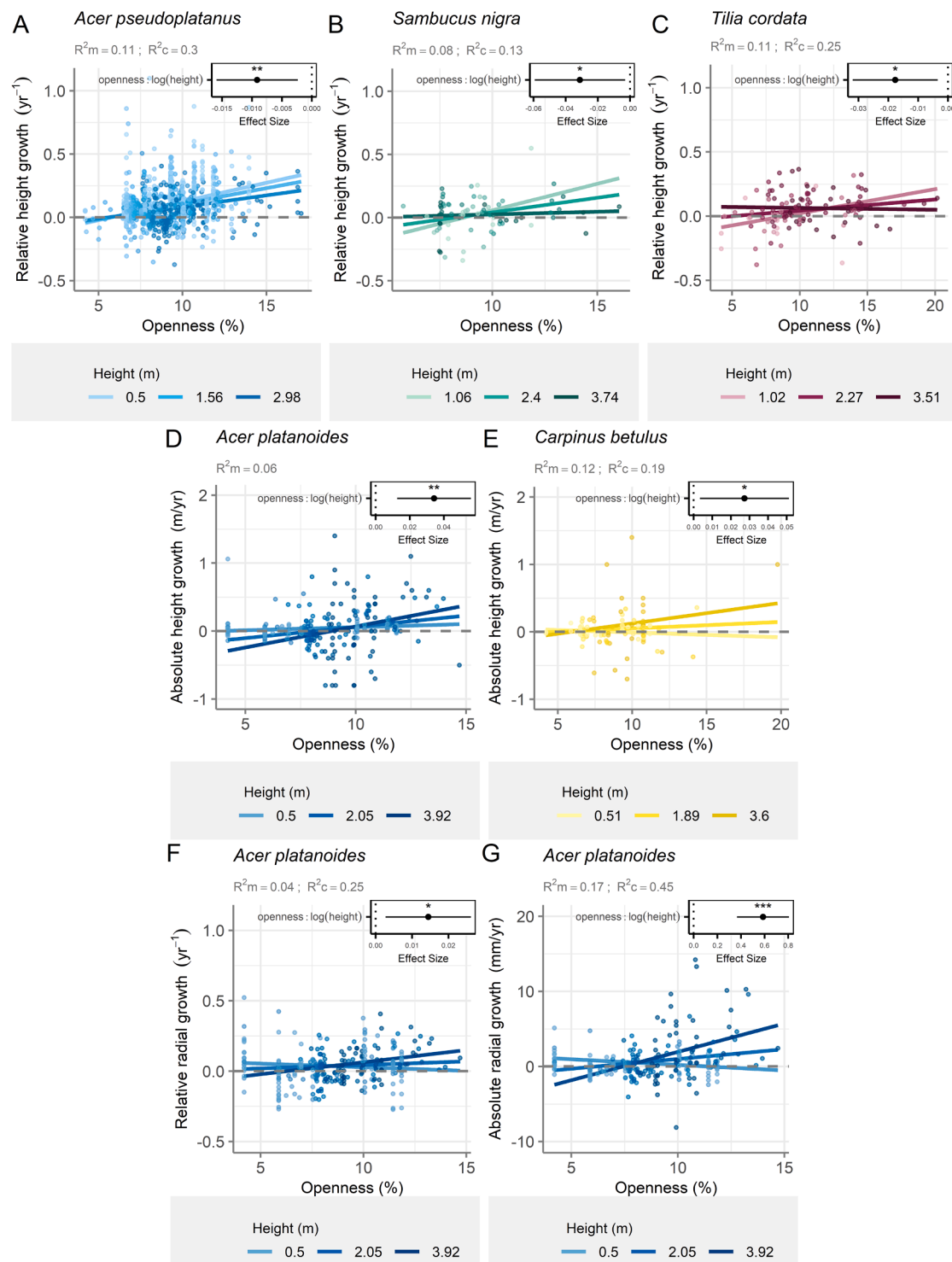


Fig. 5. Interaction effects of canopy openness and initial tree height on regeneration growth. Panels show model-based relationships for different species and growth metrics: relative height growth of (A) *Acer pseudoplatanus*, (B) *Sambucus nigra* and (C) *Tilia cordata*; absolute height growth of (D) *Acer platanoides* and (E) *Carpinus betulus*; relative radial growth of (F) *A. platanoides* and absolute radial growth of (G) *A. platanoides*. Points represent observed individual growth rates. Lines represent predictions from linear mixed-effects models at three fixed values of initial tree height (mean, mean -1 SD, mean $+1$ SD). If the mean -1 SD was smaller than the observed minimum height, the minimum height was used instead (*Acer* spp. and *C. betulus*). Tree height and openness were log- and z-transformed for model fitting; plots are shown on the original scales. Marginal and conditional R^2 values are shown above each panel. The inset displays the estimated interaction effect size with 95% confidence intervals.

growth was no longer significant.

3.3. Vitality of the regeneration

3.3.1. Forest type effect

In the dataset including four forest types, forest type had no significant effect on vitality ($\chi^2 = 3.58, p = 0.31$). In the *control* dataset with two forest types, forest type had a marginally significant main effect ($\chi^2 = 3.53, p = 0.06$) with slightly higher vitality on *mortality- control* compared to *mortality+ control* plots ($87.6 \pm 4.2\%$ vs. $76.5 \pm 6.9\%$). The final models of both data sets did not include any interaction terms with forest type. Species identity and its interactions with year and tree height had strong effects on vitality (Tables S17 and S18).

3.3.2. Effect of openness gradient

Tree vitality was influenced by canopy openness in a species-specific manner (Table 2 and S19). The overall effect was positive. *Sambucus nigra* and *T. platyphyllos* showed negative openness slopes, but with confidence intervals spanning zero (Tables S20 and S21). *Post-hoc* contrasts indicated that *A. platanooides*, *A. pseudoplatanus* and *C. betulus* had a more positive openness-vitality slope than *S. nigra*. Species identity had the strongest effect on vitality. Most trees across species exhibited normal vitality, except in *S. nigra*, where healthy and puny individuals were about equally frequent (Table S22). Most significant differences in vitality between species involved *S. nigra*, *F. excelsior*, and *Ulmus* spp., which consistently displayed lower vitality than other species (Table S23). The only additional contrast that occurred was that *A. platanooides* had higher vitality than *A. pseudoplatanus*. The vitality was significantly lower in 2022 than in 2023 and increased with tree height (Tables S19).

To assess within-species patterns, separate models were fitted. Canopy openness increased vitality in *Ulmus* spp., *F. excelsior*, *A. platanooides* and *C. betulus* but decreased it in *S. nigra* (Fig. 6, Table S24). Year effects were species-specific, with higher vitality in 2023 for *F. excelsior*, *Ulmus* spp., and *A. pseudoplatanus*. Tree height had a consistently positive effect across species, though weaker for *S. nigra* in 2023, reflecting a significant year-height interaction. Analyses of the *control* dataset, with a reduced openness gradient, confirmed the results of both the across-species and the species-specific models (Tables S25 - S27). The only difference was that openness no longer had a significant effect on vitality in *Ulmus* spp.

Vitality assessments were based on visible damage from drought

Table 2
Influence of species identity, year, openness, and tree height on regeneration vitality.

Predictor	χ^2	Num Df	<i>p</i>
openness	13.48	1	***
Tree height	152.10	1	***
year	28.55	1	***
species	221.76	7	***
Openness:tree height	-	1	-
Openness:species	28.34	7	***
Openness:year	-	-	-
Tree height:species	52.09	7	***
Tree height:year	-	-	-
Species:year	-	-	-

Notes: Results are based on a generalised mixed-effects model predicting the binomial response of tree vitality in the regeneration layer. The full model included species identity, year, openness, and initial tree height, with all two-way interactions. Higher-order interactions were not modelled due to sparse data for some combinations. Random effects accounted for the split-plot design (subplot nested in plot nested in block). Model selection was performed by comparing the AICc values of the model candidates to identify the best-fitting, most parsimonious model. The table reports ANOVA results of the final model (χ^2 , numerator degrees of freedom, and asterisks displaying *p*-values). $R^2m = 0.29$; $R^2c = 0.51$.

stress, insect feeding, browsing, and other causes such as visible fungal infections or mechanical injuries. Supplementary Figures (S13 - S16) show the distribution of these damage types by species, forest type, year, and tree size class. As expected, browsing was much more prevalent in small trees, whereas taller trees were largely unaffected. Drought damage was more frequent in 2022 than in 2023 across all forest types and size classes. Species differed slightly in their damage profiles: *S. nigra* and *Ulmus* spp. exhibited comparatively high levels of drought damage, persisting even in 2023, while *F. excelsior* and *Ulmus* spp. showed relatively little insect damage. In contrast, *F. excelsior* was more strongly affected by browsing than other species. Notably, *T. platyphyllos* was disproportionately affected by other types of damage, particularly leaf fungi and major stem breaks caused by fallen deadwood.

4. Discussion

Canopy opening proved to be a decisive driver of regeneration dynamics, accelerating the ongoing change in species composition towards an understorey dominated by sycamore maple, followed by Norway maple. Targeted small-scale interventions promoting oak regeneration may help to prevent this dominance. Increased openness generally enhanced growth across all studied tree species; however, responses in growth patterns and vitality differed markedly among them. We first address hypotheses 1 and 2 by analysing how increased openness influenced species-specific dominance and growth patterns in the regeneration. We then discuss hypothesis 3 with respect to species-specific vitality responses along the openness gradient and during the drought year. Finally, we synthesise the current competitive situation and outline potential future trajectories under climate change, management intervention and hydrological revitalisation. We conclude with study limitations and implications for forest management and conservation.

4.1. Regeneration growth dynamic along the openness gradient

Against the backdrop of ongoing canopy dieback (see Notes S1 for canopy dynamics), increased light availability enhanced growth across all investigated species, as expected in H2 and consistent with previous studies (Annighöfer et al., 2017; Bebre et al., 2021; Petriřan et al., 2009; Sevilano et al., 2016). However, the magnitude and pattern of response differed among species, reflecting distinct life-history strategies (Fig. 4).

The flood-intolerant species *A. pseudoplatanus* (52.2%) and *A. platanooides* (11.7%) together account for nearly two-thirds of the regeneration basal area (Fig. 2), considerably exceeding the 42.4% and 5.6% reported by Wirth et al. (2021) from an inventory conducted five years earlier on different plots within the same forest. Similar expansions have been observed in many other Central European forests, promoted by annual prolific seed production, effective wind dispersal, and pronounced juvenile shade tolerance enabling establishment and persistence under closed canopies (Härdtle et al., 2020; Hein et al., 2009). Increased light availability further amplified this advantage: plots with higher overstorey mortality exhibited a greater total basal area of *A. pseudoplatanus*, driven by a higher abundance of larger individuals, whereas *A. platanooides*, present in the regeneration layer of the study area only since the 20th century (Gläser, 2005), showed no significant difference in basal area between sites with high and low canopy mortality (Fig. S9). However, higher frequencies in the smallest size classes on more disturbed plots suggest an ongoing increase in recruitment (Fig. S10). Together with declining abundances of other tree species at high-mortality sites, these patterns indicate an advanced stage of structural transformation, in which the decline of characteristic flood-plain species is accompanied by the emergence of a new generation dominated by flood-intolerant maples (supporting H1).

The exceptional ability of *A. pseudoplatanus* to exploit canopy gaps was evident in our growth analysis, where it responded strongly to increasing openness across all measured growth dimensions (relative

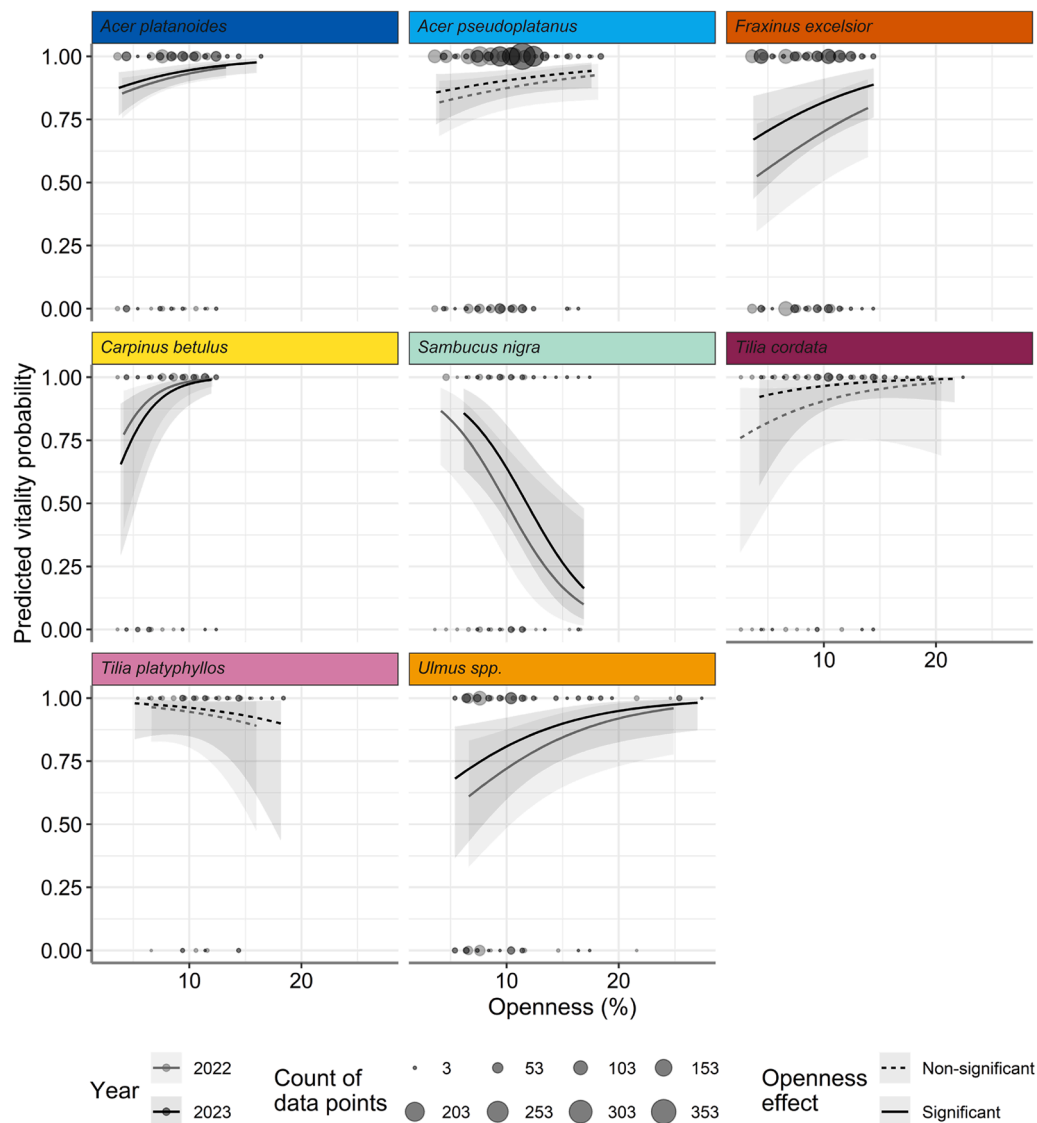


Fig. 6. Effects of canopy openness on tree regeneration vitality at mean tree height by species and year. Points represent observed individual vitality (0 = puny, 1 = normal), with size proportional to the number of trees in each bin of openness. Lines show model-predicted probability of vitality, with 95% confidence intervals. The best parsimonious model for each species was selected via AICc: simple additive binomial generalised mixed-effects model with openness, year, and tree height as fixed effects, except for *S. nigra* and *A. platanoides*, where the interaction between year and tree height was included. Plot ID was included as a random intercept. Solid/dashed line types indicate statistically significant/non-significant openness effects.

and absolute height and radial growth). Its rapid height increment allows it to secure vertical space quickly. Concentrating leaf area in the upper crown maximises light capture and reduces self-shading, reinforcing its status as a “gap specialist” (Caquet et al., 2010; Collet et al., 2008; Petriřan et al., 2009). Along the shade-tolerance gradient *A. pseudoplatanus* occupies an intermediate position (Annighöfer et al., 2017; Nagel et al., 2014). Its seedlings persist under low light (Ammer, 1996; Hättenschwiler and Körner, 2000; Kazda et al., 2000), but light demand increases markedly with size (Collet et al., 2011; Hölscher, 2004). Consequently, canopy openings are considered essential for recruitment into the upper canopy (Hein et al., 2009; Nagel et al., 2014; Petriřan et al., 2009). This combination of dense seedling banks established in shade and rapid gap exploitation confers a strong competitive advantage under current conditions. One mechanism underlying this flexibility may be pronounced leaf plasticity: Wyka et al. (2022) demonstrated that under increased light, mature leaves of *A. pseudoplatanus* thicken through elongation of palisade cells, enhancing photosynthetic efficiency and mitigating photooxidative stress. While, as to be expected, relative growth declined and absolute growth

increased with initial tree height, the effect of openness remained largely stable across size classes. Only a weak negative interaction with relative height growth suggests a gradual shift in larger saplings toward branching, root growth, or stem thickening. However, the effect was small and even advanced regeneration still showed strong vertical responses to light (Fig. 5).

Markedly different, we found for *A. platanoides* a significant positive interaction between canopy openness and tree height for both radial growth measures and for absolute height growth, mainly because smaller saplings showed almost no response to increased light (Fig. 5). This pattern fits a more shade-tolerant regeneration strategy (Martin and Marks, 2006; Petrovska et al., 2022; Reinhart et al., 2006). Small seedlings maintain conservative growth even under high light, apparently prioritising survival over rapid above-ground growth, while larger individuals, once structurally stable, respond more strongly to increased light following disturbance.

Sambucus nigra, which was also removed during thinning, is discussed separately as the only shrub species (Notes S2). For the remaining tree species, the openness gradient extended to the *thinned*

subplots. Across these species, saplings on subplots combining high overstorey mortality with understorey thinning showed the highest radial growth rates, whereas height growth varied little among forest types (Table S6). This suggests that increased light and reduced competition primarily promote stem thickening and mechanical stabilisation, a pattern commonly observed following canopy opening (Caquet et al., 2010; Kneeshaw et al., 2002; Noyer et al., 2019) and consistent with the ecology of these mostly shade-tolerant species (*Ulmus* spp., *Tilia* spp., *C. betulus*; supporting H2). Along the openness gradient, these species consistently increased radial growth irrespective of initial tree height, while height growth remained less responsive (Fig. 4). This indicates conservative allocation strategies favouring structural consolidation rather than rapid vertical extension. *Carpinus betulus* and *Ulmus* spp. exemplify this pattern: hornbeam's dense wood promotes mechanical stability, while elms in the regeneration layer are typically highly branched, shrub-like. Architectural constraints likely also shaped the growth pattern of *T. cordata*, whose seedlings typically invest in a single main axis, but larger saplings develop multi-axial crowns, limiting fast vertical elongation (Götz and Wolf, 2014). This matches our observation of a negative interaction between tree size and openness for relative height growth, opposite to the pattern found for *A. platanoides* in absolute height growth. In contrast, *T. platyphyllos* showed a steeper, albeit statistically less consistent, height growth response to light, consistent with the description by Pigott (2020) that the species maintains a vertical leading shoot for longer.

Besides sycamore maple, *F. excelsior* is also described as a light-demanding gap specialist (Annighöfer et al., 2017; Petriřan et al., 2009). Although ash can establish under shade, sustained growth requires higher light availability (Emborg, 1998; Marigo et al., 2000; Tapper, 1996). This aligns with our finding of a positive height response to openness (supporting H2), albeit weaker than that observed for sycamore maple, whereas radial growth showed no significant increase.

The three species removed during thinning (*A. pseudoplatanus*, *A. platanoides* and *S. nigra*) can resprout vigorously from stump reserves, a process potentially influencing post-treatment competition; their resprouting dynamics are analysed in the supplement (Notes S3).

4.2. Sapling vitality across light conditions and drought

Vitality increased with canopy openness for *C. betulus*, *Ulmus* spp., *F. excelsior* and *A. platanoides*, whereas the highly shade-tolerant *Tilia* spp. showed little response (supporting H3). Contrary to our expectations, *A. pseudoplatanus* did not exhibit increased vitality, and *S. nigra* even showed decreased vitality along the openness gradient despite their lower shade tolerance (Fig. 6). Across species, vitality increased with tree height, most likely reflecting decreasing browsing pressure and was overall high, except for *S. nigra* (see Notes S2).

The improved vitality of *F. excelsior* on more open plots may reflect not only higher light availability but also reduced *H. fraxineus* spore pressure, as infection risk and spore density are typically higher in dense stands due to limited air circulation, elevated humidity and potentially closer proximity to spore sources (Grosdidier et al., 2018, 2020; Martin et al., 2025). Not only in the canopy (Notes S1), but also in the regeneration layer, ash showed the highest annual mortality rate with 13.6% (Fig. S6). Seedlings may remain symptomless due to short exposure times, whereas saplings often experience the highest mortality, as the fungus spreads more rapidly through their limited tissue than in larger trees (Bengtsson et al., 2021; Enderle et al., 2017; Timmermann et al., 2017). Furthermore, since many ascospores emerge from apothecia on fallen petioles, spore pressure is particularly high near the forest floor (Chandelier et al., 2014; Dvořák et al., 2023). In line with this, *F. excelsior* showed the lowest mean (1.17 m) and median (0.89 m) height of all species, and no individuals exceeded 34 mm root-neck diameter in the regeneration layer, indicating high germination but low survival (Table S1, Fig. S9). While additional mortality factors, such as the recorded severe browsing (Fig. S15, see also Detsch et al., 2025;

Turczański et al., 2021), cannot be excluded, *H. fraxineus* infection remains the plausible primary cause of the decline in established ash regeneration.

Dutch elm disease primarily affects larger trees, as bark beetles typically select individuals > 10 cm DBH (Brunet et al., 2023; Hytteborn et al., 2017). Consequently, unlike ash, elms can reproduce before reaching this size and also regenerate vegetatively through root suckers, enabling them to persist in the regeneration and understorey despite their near disappearance from the overstorey (Koop, 1987; Thomas et al., 2018). Owing to its higher tolerance to Dutch elm disease, *U. laevis* has been increasingly discussed as a potential component of future forest compositions (Kavaliauskas et al., 2023; Mackenthun, 2004; Schmucker et al., 2023). However, our pooled *Ulmus* spp. dataset showed significantly lower vitality in the drought year 2022, consistent with classifications of *U. laevis* saplings as drought sensitive and supporting H3 (Niinemets and Valladares, 2006; Thom et al., 2026). Because drought tolerance differs among elm species, with *U. minor* classified as drought-tolerant and *U. glabra* as intermediate (Niinemets and Valladares, 2006), our results represent an aggregate response and may obscure species-specific differences. In contrast, *C. betulus* and *Tilia* spp. maintained stable vitality across years, consistent with their classifications as moderately to strongly drought-tolerant (Thom et al., 2026) and a growth strategy characterised by slow height increment and a stronger allocation to radial growth (supporting H2 and H3).

Rapid above-ground growth can confer a competitive advantage in dense stands, but often comes at the expense of root growth, reducing water and nutrient access as well as mechanical stability (Annighöfer et al., 2017; Chen, 1997; Petriřan et al., 2009). This trade-off may partly explain the different regeneration strategies of the two maple species: *A. pseudoplatanus* displayed fast above-ground growth but reduced vitality during drought and consistently lower vitality than *A. platanoides*, which grew more conservatively yet maintained stable vitality across both years. While an increase in root-to-shoot ratio is a common drought response across tree species (Brunner et al., 2015; Poorter et al., 2012), Carón et al. (2015) found greater root biomass in *A. platanoides* seedlings compared to *A. pseudoplatanus* across different temperature and moisture conditions, and also Kunz et al. (2016) described a high root-to-shoot ratio for *A. platanoides* seedlings under varying drought treatments. This inherent predisposition toward below-ground investment in seedlings is probably an advantage under water-limited conditions.

For all species with reduced vitality in 2022 (*A. pseudoplatanus*, *F. excelsior*, *Ulmus* spp.), the drought year effect did not change across openness conditions (Table S24), consistent with our previous finding that more open subplots were only slightly warmer and showed minimal differences in topsoil moisture across sites differing in canopy mortality and understorey treatment (Lenk et al., 2024).

4.3. Present winners and future trajectories of tree regeneration

Currently, *A. pseudoplatanus* dominates the regeneration layer, a position strengthened by rapid height growth under increased canopy openness, enabling it to exploit newly formed gaps. Although its long-term prospects may be weakened by susceptibility to sooty bark disease, massive seed production and dense regeneration currently compensate for the pathogen-related mortality by replacing diseased individuals with conspecific seedlings, thereby reinforcing its dominance in the regeneration. Other species, like *C. betulus* or *Tilia* spp., are disadvantaged due to their slower height growth. *Fraxinus excelsior* follows a similar gap-oriented regeneration strategy as sycamore maple but shows considerably lower seedling abundance and height growth, which, together with strong browsing pressure and high susceptibility to ash dieback, limits its current competitive potential. Natural oak regeneration taller than 50 cm was almost absent in our inventories (Fig. 2, S6), underlining a substantial risk of losing this hardwood floodplain key species (see also Wirth et al., 2021). Seedlings rarely

survive beyond the first years, likely due to insufficient understorey light and strong competition from the dense maple-dominated regeneration layer. Accordingly, reducing dense shading is not merely beneficial but essential to sustain viable oak populations, as shown by high mortality of planted seedlings in dense understorey despite severe overstorey dieback, whereas vigorous development occurred on sites combining high canopy mortality with targeted understorey thinning (Lenk et al., 2025). However, whether natural regeneration will establish under these conditions remains open, as regeneration success also depends strongly on seed dispersal, predation and browsing (but see Tinya et al., 2025).

Without silvicultural or hydrological interventions, and given the large number of seed trees in the forest and surrounding area, we expect the flood-intolerant sycamore maple to continue dominating the regeneration layer under current conditions, with an increasing admixture of Norway maple. The third native maple species, field maple (*A. campestre*), occurred only sporadically (six canopy trees, one sapling), restricting an assessment of its competitive potential. Nevertheless, the species combines high tolerance to both flooding and drought and is therefore often considered a relevant species under future climate scenarios (Kunz et al., 2016; Schmucker et al., 2023; Walentowski et al., 2017). Based on independent canopy inventories in the Leipzig floodplain forest, Elles et al. (2025) predicted an increase in relative dominance of field maple under moist conditions, Norway maple under dry conditions and hornbeam under intermediate site conditions over the next century. On our plots, *C. betulus* was more frequent than field maple (canopy: 9.2%, regeneration: 2.9%) and has been shown to expand rapidly in other meliorated European floodplain forests (Brzeziecki et al., 2020; Janik et al., 2011). Its moderate drought tolerance, high shade tolerance (Sikkema et al., 2016) and stable vitality on our plots support the projection that it could gain competitive importance if the dominance of *A. pseudoplatanus* is reduced, a potential further supported by its positive vitality response to increased canopy openness (Fig. 6). At present, less competition could also favour *Tilia* spp., which showed consistently vital regeneration across openness conditions and years, were little affected by browsing (Fig. S15) and currently show no evidence of major pathogen pressure (see also Jaeger et al., 2016; Radoglou et al., 2008). Despite the much lower number of *T. platyphyllos* in the overstorey (12 vs. 80 trees with DBH $\geq$ 20 cm), both *Tilia* spp. contributed similarly to regeneration basal area (Fig. 2). This reflects favourable establishment conditions during decades without flooding, even for the more flood-sensitive *T. platyphyllos* (Glenz et al., 2006; Niinemets and Valladares, 2006; Radoglou et al., 2008).

4.4. Study limitations

While the study provides important short-term insights into regeneration dynamics under canopy dieback and management interventions, study limitations should be acknowledged. First, the low number of observations for rarer species limited statistical power. Interactions between forest type and species identity could not be tested, and the structure of the binomial models limited the inclusion of higher-order interactions due to unbalanced and sparse data for some species. In addition, the evaluation of size-dependent effects was constrained by the observed size distributions; for example, no taller *F. excelsior* saplings were recorded. Second, the study covers only a single year of regeneration development. This short time frame restricts the detection of delayed or cumulative growth responses and limits the ability to capture newly established seedlings.

5. Conclusion & application

Our study demonstrates that drought- and pathogen-induced canopy dieback, and structural changes from understorey thinning, fundamentally reshape regeneration dynamics in the Leipzig floodplain forest. Although all studied tree species benefited from the gap-related light

availability in growth and partly vitality, our results align with previous studies in which canopy openings favoured primarily highly competitive species rather than promoting diversification, even though gap characteristics and site conditions remain decisive for the eventual species composition (Caquet et al., 2010; Collet et al., 2008; Detsch et al., 2025; Kwit and Platt, 2003; Tinya et al., 2025). The current canopy openings have accentuated competitive asymmetries favouring *A. pseudoplatanus* and *A. platanoides*, both of which combine pre-established regeneration with strong post-disturbance growth responses, allowing them to pre-empt light resources over slower or less abundant species. Consequently, without intervention, the current combination of canopy gaps and lack of hydrological restoration leads to a severe depletion of biodiversity in the regeneration layer and potentially across the entire ecosystem. To counter this trend, our results show that small-scale understorey thinning, i.e. removing the flood-intolerant *A. pseudoplatanus*, *A. platanoides* and *S. nigra* (see Notes S3 for resprouting responses), on sites with high canopy mortality is beneficial not only for promoting planted oak seedlings (Lenk et al., 2025) but also for supporting the naturally regenerating tree species diversity. Under current conditions, species with low susceptibility to drought and pathogen pressure, particularly *Tilia* spp. and *C. betulus*, are most likely to benefit from such measures. Although both are highly capable of resprouting, traditional coppice-with-standards management would probably not favour them under the present conditions in the same way. The comparatively long intervals between coppicing cycles (typically ca. 10–40 years; Unrau et al., 2018) would likely be too long to prevent rapid reclosure of the understorey by *A. pseudoplatanus* and *A. platanoides* through vigorous resprouting and rapid gap exploitation. As a result, regeneration opportunities for less competitive species, and especially for *Q. robur*, would remain limited. A similar pattern was also observed following a local attempt to establish a coppice-with-standards system in Leipzig in 2007, which resulted in strong maple dominance and reduced tree species diversity within a few years (pers. obs.).

Even though the first thinning in our experiment inevitably removed some non-target species within the dense maple understorey, subsequent maintenance becomes considerably easier once the stand is more open. Furthermore, restoring sustainable flood dynamics will likely drastically reduce the management effort required to maintain high species diversity, as long as a considerable proportion of flood-tolerant tree species still exist in the regeneration layer alongside the highly flood-sensitive species sycamore maple, Norway maple and elder (Notes S3). Maintaining biodiversity is widely recognised as fundamental for ecosystem resilience, as species-rich communities have a greater capacity to withstand future disturbances and environmental change (Jactel et al., 2017; Messier et al., 2022; Silva Pedro et al., 2015). Consequently, our findings emphasise the need for adaptive management in the floodplain forest to preserve the still exceptionally high, yet declining, tree species diversity. This is particularly relevant for pedunculate oak, a key species for biodiversity that is currently maintained almost exclusively through planting. While many of our observed patterns align with expected responses related to shade or drought tolerance, several effects were size-dependent, underscoring the importance of considering ontogenetic variation when assessing regeneration dynamics. Moreover, interactions between species traits and environmental conditions introduce substantial uncertainty into predictions of future forest development under rapidly changing conditions. In this context, sustained scientific monitoring provides a critical foundation for adaptive management. Given the short-term nature of this study and the inherent heterogeneity of observational field experiments, extending observations over longer periods and complementing them with controlled experimental approaches (e.g. restricted age classes, controlled light and microclimatic conditions) may further help disentangle species-specific drivers, delayed responses and establishment patterns under changing environmental and management conditions.

CRediT authorship contribution statement

Annalena Lenk: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Melanie Hanfstängl:** Writing – review & editing, Investigation, Data curation. **Sophia Waha:** Writing – review & editing, Investigation, Data curation. **Christian Wirth:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Funding

This work was supported by a scholarship granted to Annalena Lenk by the German Federal Environmental Foundation (DBU, grant number: 20021/740-35/4).

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Annalena Lenk reports financial support was provided by the German Federal Environmental Foundation (DBU). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank our colleagues and student assistants for their help in establishing the experimental setup and collecting data, with special thanks to Julia van Braak, Tom Künne, and Max Neumann for their great support. We are grateful to the Leipzig Forestry Department and the Saxony State Forestry Service for assistance in selecting research plots, and we acknowledge the responsible State Environmental Office of Leipzig for providing the necessary permits for fieldwork. We appreciate the support from Leipzig University for Open Access publishing.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123791.

Data availability

The data and R code used in this study are available on Zenodo: doi.org/10.5281/zenodo.19385416

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