

## Supporting conservation planning in a national biodiversity hotspot – Projecting species composition across a groundwater level gradient using a demographic forest model

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### ARTICLE INFO

#### Keywords:

Alluvial forest  
Groundwater table  
Oak regeneration  
PPA model  
*Quercus robur*  
Re-vitalization measures

### ABSTRACT

The Leipzig floodplain forest is a biodiversity hotspot of national significance. However, it is an urban forest heavily impacted by human activities, including the alteration of the hydrological regime preventing floods and leading to a lower groundwater level. In parts of the Leipzig Floodplain Forest, the restoration of a near-natural hydrological regime with regular floods and a raise of the groundwater level is considered. However, it is unclear whether raising the groundwater level in particular would ensure the long-term conservation of typical floodplain tree species such as European ash (*Fraxinus excelsior*) and pedunculate oak (*Quercus robur*), which are considered key species for biodiversity conservation. To investigate this question, we quantified the relationships between groundwater table distance and the growth, mortality, and recruitment rates for eight common tree species in the Leipzig Floodplain Forest using forest inventory data from 60 plots and a spatial groundwater model. Based on these relationships, we simulated the long-term dynamics of species composition with and without a raise of the groundwater table using the Perfect Plasticity Approximation (PPA) forest model.

Under current groundwater conditions, the model projected a substantial decline of the typical floodplain species ash and oak over 100 years. Field maple (*A. campestre*) and hornbeam (*Carpinus betulus*) benefited from this decline, as did the less flood-tolerant Norway maple (*A. platanoides*) on dry sites. When a raise of the groundwater level was simulated, ash and oak continued to decline. However, *A. platanoides*, which is not a typical floodplain forest species, was projected to be inhibited by a raise of the groundwater level. These results suggest that a raise of the groundwater table alone does not lead to the conservation of ash and oak, and hence the rich biodiversity associated with them. The study illustrates how ecological modeling can support the evaluation of biodiversity conservation strategies and provide the scientific basis for the successful transformation of this unique ecosystem towards a self-sustained biodiversity-rich urban forest.

### 1. Introduction

Floodplain forests provide extraordinarily diverse habitats for many plant and animal species and therefore play a crucial role in preserving biodiversity (Gregory et al., 1991; Crow et al., 2000; Klimo and Hager, 2001; Schnitzler et al., 2007; Havrdová et al., 2023). They also provide

important ecosystem services on a global and local level, such as flood retention, temperature buffering, and carbon storage (Klimo and Hager, 2001; Pramova et al., 2012; Ellison et al., 2017; Potapov et al., 2017; Riis et al., 2020; Havrdová et al., 2023). However, the conservation status of floodplain forests in Germany is assessed to be unfavourable to poor (BfN, LRT 91F0\*), and at the European scale, floodplain forests rank

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<https://doi.org/10.1016/j.ecolmodel.2024.110996>

Received 31 May 2024; Received in revised form 29 November 2024; Accepted 12 December 2024

Available online 22 December 2024

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among the most endangered ecosystems (Leuschner & Ellenberg, 2017; Mikac et al., 2018).

The Leipzig Floodplain Forest (LFF), Germany's second-largest urban floodplain forest, stands out for its structural diversity and species richness (Engelmann et al., 2019; Wirth et al., 2021; Scholz et al., 2022). The predominantly occurring *Quercus-ulmetum minoris* (LRT 91F0\*) hardwood forest, dominated by European ash (*Fraxinus excelsior* L.), pedunculate oak (*Quercus robur* L.), and sycamore maple (*Acer pseudoplatanus* L.; Engelmann et al., 2022; Henkel et al., 2024), is designated as a Special Area of Conservation under the EU Habitats Directive. The forest provides habitat for European wild cat, eleven bat species, 105 species of breeding birds, and 442 beetle species (Wirth et al., 2021; Haack et al., 2022). A significant proportion of these beetle species, particularly those listed in the Red List and relict species associated with primeval forests, depend on the occurrence of large *Q. robur* and *F. excelsior* trees (Haack et al., 2021). This makes them key species for biodiversity conservation (Engelmann et al., 2019; Wirth et al., 2021).

The need for an effective biodiversity conservation strategy is underscored by the current rapid transition in species composition, especially the decline of *Q. robur* and *F. excelsior* (Engelmann et al., 2019; Wirth et al., 2021, 2022). One reason for this decline is the altered fluvial dynamics caused by the construction of the "Neue Luppe" drainage channel in 1936, which disrupted the natural flooding regime and lowered the groundwater levels by 1.5–2 m (Scholz et al., 2022). It impeded natural oak regeneration, while less drought- but shade-tolerant maple seedlings benefited from the altered fluvial dynamics (Engelmann et al., 2019). Additionally, ash dieback and sooty bark-disease caused declines in *F. excelsior* and *A. pseudoplatanus*, respectively (Wirth et al., 2021; Henkel et al., 2024), and recent consecutive drought years with extreme heatwaves lead to increased physiological stress of trees in the LFF (Schnabel et al., 2022).

To halt the decline of the typical hardwood floodplain tree species, a comprehensive hydrological restoration of the Northern LFF is planned to raise groundwater levels and restore natural flooding dynamics (Engelmann et al., 2019; Wirth et al., 2021). However, it is unclear how the species composition will change in the future both under current and raised groundwater levels, and whether a hydrological restoration would be sufficient for preserving the imperiled overstorey species *Q. robur* and *F. excelsior* (Wirth et al., 2021), or if additional management measures are required to maintain the characteristic species composition. To address these questions and support conservation planning, forest succession models offer a great – but often overlooked – potential. While forest models have been used to support efficient forest management (Hansen et al., 1995; Rüger et al., 2007; Torano Caicoya et al., 2018), their application in mixed-species uneven-aged forests and for conservation purposes remains rare. This study aims to address this challenge and to explore the effects of raising groundwater levels on species composition in the LFF using a demographic forest model.

Information on species-specific responses of demographic rates to groundwater levels in hardwood floodplain forests is limited (Gee et al., 2014; Senfeldr et al., 2021). Studies often focus on a few species, often oak and ash (Stojanović et al., 2015; Skiadaresis et al., 2019; Senfeldr et al., 2021; Szatniewska et al., 2022), while disregarding other important tree species. Moreover, most research is carried out on tree growth, whereas recruitment and mortality rates are less often reported. However, a comprehensive understanding of the influence of groundwater levels on tree demography is essential for informed conservation planning (Hughes et al., 2012; Szatniewska et al., 2022). Here, we leverage forest inventory data and a spatial groundwater model from a scientific monitoring project in the LFF (Seele-Dilbat et al., 2022) to quantify growth, mortality, and recruitment rates across a groundwater gradient for the eight most abundant tree species.

These demographic rates are used to parameterize the Perfect Plasticity Approximation (PPA) model (Purves et al., 2008), a demographic forest model that simulates the height-structured competition for light between the tree species. The PPA model has been shown to provide

accurate predictions of forest dynamics and changes in species composition in both temperate and tropical forests (Purves et al., 2008; Rüger et al., 2020). Here, our objective is to support forest biodiversity conservation planning by applying a demographic forest model to project the consequences of a raise of the groundwater table for the growth, mortality, and recruitment rates of tree species and for the resulting species composition in the LFF. Understanding potential consequences of the proposed hydrological restoration measures provides the scientific basis for the successful transformation of this unique ecosystem towards a self-sustained biodiversity-rich urban forest.

## 2. Methods and materials

### 2.1. Study site and forest inventory data

The study site is a *Quercus-Ulmetum minoris* floodplain forest situated in the northwestern segment of the Leipziger Elster-Luppe floodplain (Fig. 1). The study area encompasses 2830 ha in the LFF. This forest is classified under the FFH habitat types of hardwood floodplain forest (LRT 91F0\*) and chickweed-oak-hornbeam forest (LRT 9160, Seele-Dilbat et al., 2022). The focal tree species used in this study include European ash (*Fraxinus excelsior* L.), pedunculate oak (*Quercus robur* L.), sycamore maple (*Acer pseudoplatanus* L.), lime (*Tilia* spp.), hornbeam (*Carpinus betulus* L.), elm (*Ulmus* spp.), field maple (*Acer campestre* L.), and Norway maple (*Acer platanoides* L.; Engelmann et al., 2022).

We used inventory data from 60 permanent forest plots of the scientific monitoring of the "Lebendige Luppe" project (Rieland et al., 2024; Seele-Dilbat et al., 2022). The plots (Fig. 1) were selected using a stratified random design and are located within the morphological floodplain. They are 2500 m<sup>2</sup> in size, and most of them have a perimeter of 50×50 m. The forest stands on these plots are ≥80 years old (Seele-Dilbat et al., 2022). Forest inventory data were collected for 31 plots in 2013 and 2020, and for the other 29 plots in 2016 and 2020. Trees with diameter at breast height (dbh) ≥5 cm were surveyed using a tachymeter for accurate height and location measurements. Recorded data for each tree included dbh, total height, species, and whether trees had survived the interval. The dataset comprises 8491 individual trees. Individuals classified as *Ulmus minor* MILL., *Ulmus glabra* HUDS., and *Ulmus* spp. in the inventory data were pooled and treated as *Ulmus* spp. in the analyses. Individuals classified as *Tilia cordata* MILL. and *Tilia platyphyllos* SCOP. in the inventory data were pooled and treated as *Tilia* spp.

### 2.2. Distance to groundwater level

The distance to groundwater level (DTG) was calculated at both the plot and tree levels because recruitment rates are calculated at the plot level, while mortality and growth are observed at the tree level. At the plot level, the median DTG was derived using groundwater data from the "Lebendige Luppe" project (Seele-Dilbat et al., 2022). Between 2014 and 2018, 34 out of the 60 plots were equipped with groundwater monitoring wells, each with a drilling depth of approximately 4 m. Data loggers recorded DTG every 30 min. Together with a digital terrain model generated through a tachymeter, the median DTG for each plot was determined. For the remaining 26 plots lacking groundwater monitoring wells, groundwater table data from the nearest monitoring well was extrapolated. The plots were subsequently categorized into three classes, each consisting of 20 plots, based on their median DTG (Table 1): plots with a DTG ≤1.6 m were classified as moist, plots with a DTG ≥2.0 m were classified as dry, all other plots were classified as intermediate. A summary of the DTG per plot is available in Table S1.

To account for differences in elevation within the plots (Kirsten et al., 2022), the DTG was determined for each tree individually. This involved intersecting a groundwater model with the spatial coordinates of individual trees and the respective elevation at the trunk base. The groundwater model incorporates the groundwater logger data for

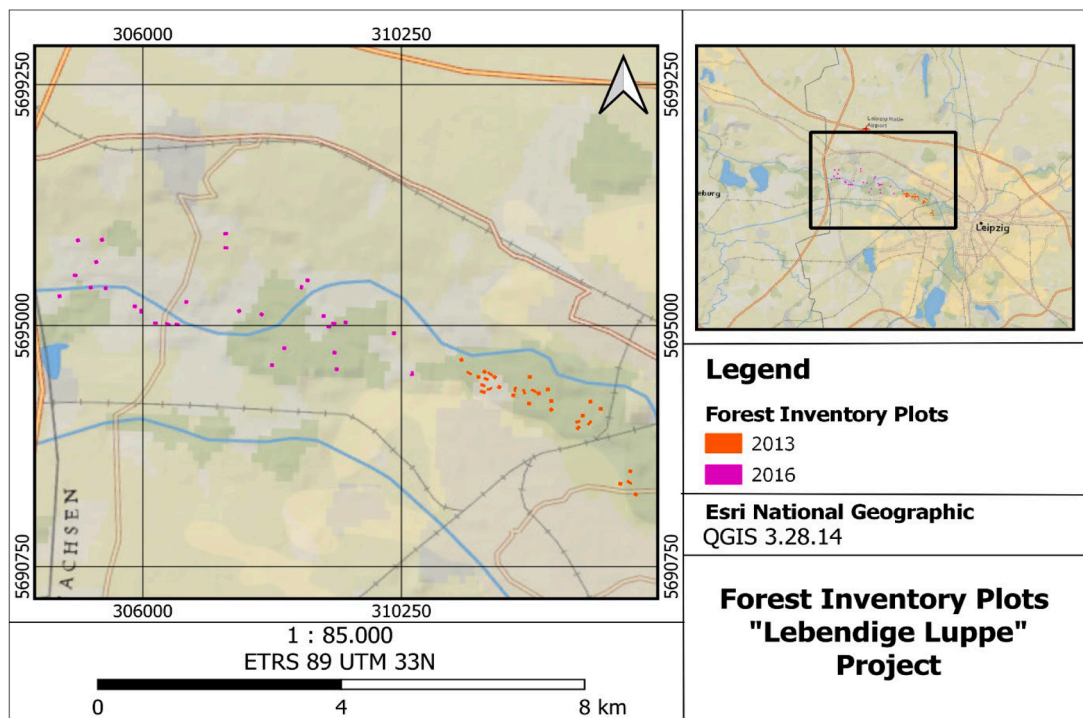


Fig. 1. Location of forest inventory plots of the “Lebendige Luppe” project differentiated by year of the first forest census.

Table 1

Groundwater classes by distance to groundwater level (DTG) for the years 2014–2022.

Class	DTG (m)				
	Median	Max	Min	Increase by 0.5 m	Increase by 1 m
Dry	2.3	3.2	2.0	1.8	1.3
Intermediate	1.8	1.9	1.6	1.3	0.8
Moist	1.3	1.6	0.5	0.8	0.3

2014–2022. For this study, the annual mean values are used and averaged over the years between the consecutive inventories. For the year 2013, during which groundwater logger data were not available, the DTG was derived from the groundwater model, which incorporated data from the years 2014–2020.

### 2.3. The PPA model

The PPA model is a demographic forest model that tracks the fate of individual trees in cohorts based on a small set of demographic rates (growth, mortality, and recruitment) and accounts for height-structured competition for light by distinguishing two discrete canopy layers: the overstory layer, where trees have access to light, and the understory layer, where trees are shaded (Purves et al., 2008; Strigul et al., 2008). Trees are assigned to the canopy layers based on their size and the size of their neighbors. The tallest trees are assigned to the overstory layer as long as their cumulative crown area does not exceed the simulation area. Smaller trees are assigned to the understory. Canopy gaps created by the mortality of overstory trees are filled by the tallest trees from the understory layer regardless of their horizontal position (perfect plasticity assumption, Strigul et al., 2008). Trees in the two canopy layers are assigned distinct growth and mortality rates for each tree species, since trees typically have higher diameter growth rates and lower mortality rates in the overstory layer than in the understory layer. The recruitment of new trees is assumed to occur at a constant rate per year and ha (Rüger et al., 2020). Trees of the same species that establish in the same

year are assigned to the same cohort and share the same diameter at breast height (dbh) and crown diameter. However, cohorts may be split in two at the transition from the understory to the overstory layer if the canopy space that was freed up by mortality in larger cohorts is not large enough to accommodate the crown area of all individuals in the cohort. Details of the model can be found in the original publications (Purves et al., 2008; Strigul et al., 2008). The PPA model has been successfully applied to predict changes in species composition and size structure in temperate and tropical forests (e.g. Purves et al., 2008; Rüger et al., 2020).

### 2.4. Model parameterization

#### 2.4.1. Canopy layer assignment

To calculate demographic rates for the over- and understory, all monitored trees were assigned to a canopy layer based on their size and the size of neighboring trees (Purves et al., 2008). To accomplish this, we manually divided the plots into four subplots with a size range of 572–677 m<sup>2</sup> per subplot because some plots were not exactly quadratic. Each tree was assigned to a subplot based on its spatial coordinates. Using allometric equations derived from dbh and crown area data of 1316 trees in the “Hainich Nationalpark” (Holzwarth et al., 2015; Supplementary material), we computed the crown area for each tree. Beginning with the largest trees per subplot, we assigned them to the overstory layer, as long as their cumulative crown area did not exceed the total area of the subplot. Smaller trees were assigned to the understory layer.

#### 2.4.2. Response of demographic rates to DTG

We calculated demographic rates separately for trees (growth, mortality) and plots (recruitment) first measured in 2013 (3367 trees, Table S2) and 2016 (3049 trees, Table S3), respectively.

The recruitment rate is defined as the number of individuals per focal species ( $s$ ) which grow over the threshold of 5 cm dbh in the plots of the three groundwater classes (g, “moist”, “intermediate”, “dry”). This number is then scaled to the plot area in each groundwater class and the length of the census interval ( $t$ ) to yield the number of recruits per ha

and year

Growth and mortality rates were calculated separately for the overstorey and understorey layer ( $l$ ). The annual diameter growth rate (cm dbh/year) for each individual tree  $i$  was calculated as the change in dbh between the consecutive censuses divided by the number of years between the consecutive censuses.

$$\text{annual growth}_{i,s,l,t} = \frac{\text{dbh}_{i,s,l,2020} - \text{dbh}_{i,s,l,\text{first inventory}}}{\text{years between censuses}_t} \quad (1)$$

We used a linear model to quantify the response of growth to DTG,

$$\text{annual growth}_{i,s,l,t} = \beta_{0s,l,t} + \beta_{1s,l,t} \times \text{DTG}_{i,s,l,t} + \varepsilon \quad (2)$$

The linear model was independently fit for each unique combination of species  $s$ , canopy layer  $l$ , and observation interval  $t$ . We used the model to determine the growth rate at the median DTG value of the three groundwater classes “moist” (1.3 m), “intermediate” (1.8 m), “dry” (2.3 m), respectively (Table 1). Additionally, we determined the growth rate at DTG values for “wet” (0.8 m) and “very wet” (0.3 m) conditions.

To calculate mortality rates, a logistic regression model was employed to quantify the response of mortality to DTG

$$\left( \frac{m_{s,l,t}}{1 - m_{s,l,t}} \right) = \gamma_{0s,l,t} + \gamma_{1s,l,t} \times \text{DTG}_{i,s,l,t} + \varepsilon \quad (3)$$

where  $m_{s,l,t}$  is the mortality probability. The logistic regression was independently fit for each unique combination of species, canopy layer, and observation interval. The binomial family with a logit link function was used in the analysis. Predicted probabilities were then converted into annual mortality rates by dividing the mortality rate by the number of years between the consecutive censuses.

$$\text{annual mortality}_{s,l,t} = \frac{-\log(1 - m_{s,l,t})}{\text{years between censuses}_t} \quad (4)$$

We used the model to determine the mortality rate at the mean DTG value of the three groundwater classes “moist” (1.3 m), “intermediate” (1.8 m), “dry” (2.3 m), respectively (Table 1). Additionally, we determined the mortality rate at DTG values for “wet” (0.8 m) and “very wet” (0.3 m) conditions.

In addition to the rates from the two census intervals, we also calculated “combined rates” as the mean value of the rates for both census intervals at the five discrete DTG values. Due to the low abundance of *A. campestre* in the plots measured in 2013 (Table S2) and of *A. platanoides* in the plots measured in 2016 (Table S3), no growth and mortality rates were calculated for these species for the intervals 2013–2020 and 2016–2020, respectively. For the “combined rates” of *A. campestre* and *A. platanoides*, we used growth and mortality rates of the census interval, for which demographic rates could be calculated. Similarly, *Q. robur* had a very low abundance in the understorey, and it was not possible to quantify the response of growth to DTG in both observation intervals (Tables S2,S3). Instead, we used the average growth rate of all *Q. robur* understorey individuals in all plots across both observation intervals as a substitute. Likewise, the low abundance of *Q. robur* in the understorey prevented the quantification of a mortality rate in the census interval 2013–2020 for this species. Instead, we used the average mortality rate of *Q. robur* from 2016 to 2020, in both observation intervals independent of groundwater class.

## 2.5. Projections of forest dynamics based on current and raised groundwater levels

We devised nine scenarios to assess changes in species composition in the LFF given the observed demographic rates of the different census intervals (2013–2020, 2016–2020, “combined rates”) under current groundwater conditions in the three groundwater classes (“moist,” “intermediate,” and “dry”). The scenarios simulated the species composition in terms of basal area of trees assigned to the overstorey and

understorey, respectively. The initial states for each scenario reflect the forest structure and species composition during the year of the first inventory. To do this, the number of individuals  $\geq 5$  cm dbh per ha and species was aggregated into 1-cm dbh classes (Boyce et al., 2025). In the case of the “combined rates” scenario, the initial state was derived from the year 2020. To validate the model, we compared the simulated overstorey basal area ( $\text{m}^2/\text{ha}$ ) after seven years (2013–2020) and four years (2016–2020) to the observed overstorey basal area ( $\text{m}^2/\text{ha}$ ) in 2020 in the plots of the respective groundwater class. To assess the sensitivity of model results to the demographic rates of the tree species, we also computed a measure of late-successional dominance,  $D^*$ , i.e. the diameter at which trees transition from the understorey to the overstorey in an equilibrium monoculture (Purves et al., 2008, Supplementary material). We then explored the sensitivity of  $D^*$  against variation in demographic rates.

We also formulated six additional scenarios to project the impact of a raise of the groundwater level on the species composition of the LFF. These scenarios exclusively use the “combined rates” for the three groundwater classes (“moist,” “intermediate,” and “dry”) with a 0.5 m (at 0.8 m, 1.3 m, and 1.8 m) and 1 m (at 0.3 m, 0.8 m, and 1.3 m) raise of the groundwater level (Table 1). The initial state from 2020 is used. As recruitment rates for “wet” and “very wet” groundwater conditions we used the recruitment rates observed for the “moist” groundwater class.

All analyses were carried out with R version 4.2.1 (R Development Core Team, 2022). The model code, scripts used for analyses, the demographic rates and initial states for all model scenarios are available at [https://github.com/lucian-elles/Elles\\_et\\_al\\_2024\\_Supporting\\_conservation\\_planning\\_in\\_a\\_national\\_biodiversity\\_hotspot](https://github.com/lucian-elles/Elles_et_al_2024_Supporting_conservation_planning_in_a_national_biodiversity_hotspot).

## 3. Results

### 3.1. Response of demographic rates to DTG

*A. pseudoplatanus*, *A. campestre* (2016–2020), *Tilia* spp. (2013–2020), and *Ulmus* spp. had high recruitment rates, while *C. betulus* and *F. excelsior* had low recruitment rates and *Q. robur* had no recruits (Fig. 2). Recruitment rates were relatively insensitive to DTG, except for increased recruitment of *A. pseudoplatanus* in dry sites in 2013–2020 and low recruitment of *C. betulus* in dry sites.

Overall, *Acer* spp. and *C. betulus* grew relatively fast, whereas *F. excelsior* and *Tilia* spp. grew rather slowly. The response of growth rates to DTG differed between species (Figs. 3, S1), but only few relationships were statistically significant (Table S4). *F. excelsior* grew slower in moist sites in the overstorey (Fig. 3a,b). *Q. robur* grew slower in moist sites in the overstorey in 2013–2020, but not in 2016–2020. *A. pseudoplatanus* grew faster in moist sites (Fig. 3b,e), statistically significantly so in the understorey in 2016–2020. *C. betulus* grew faster in moist sites in the understorey in 2013–2020. Growth rates of *A. campestre*, *A. platanoides*, *Tilia* spp., and *Ulmus* spp. responded only weakly to DTG.

Mortality rates were higher in the understorey compared to the overstorey (Fig. 4). *F. excelsior*, *A. pseudoplatanus*, and *Ulmus* spp. had high mortality rates, whereas *Tilia* spp., *C. betulus*, and *A. campestre* had low mortality rates (Table S5, Figs. 4, S2). In 2013–2020, all species except for *Tilia* spp., had higher mortality rates in moist sites than in dry sites in the overstorey (Fig. 4a), statistically significantly so for *A. pseudoplatanus*, *A. platanoides*, and *F. excelsior* (Table S5). In the understorey, only *A. platanoides* showed higher mortality rates in moist sites (Fig. 4d). In 2016–2020, *A. pseudoplatanus* (overstorey), *Q. robur* (overstorey), and *Tilia* spp. had higher mortality rates in dry sites (Fig. 4b).

### 3.2. Projections of forest dynamics based on current and raised groundwater levels

Model projections were generally in agreement with observations after seven (Fig. 5a-c) or four years (Fig. 5d-f). Without changes in groundwater levels, the model projected a substantial reduction in

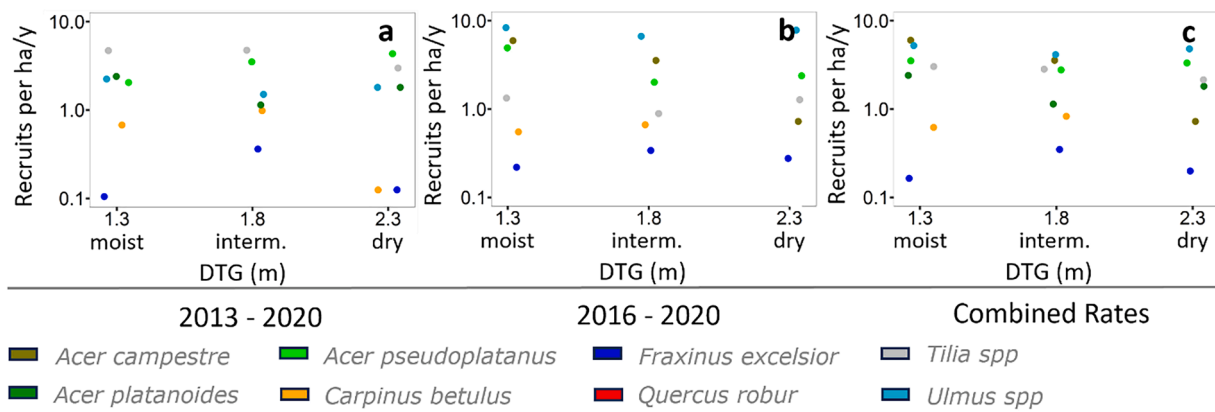


Fig. 2. Annual recruitment rates (number of individuals that exceed the dbh threshold of 5 cm per ha) for eight focal species for the three groundwater classes: moist (~1.3 m distance to groundwater DTG), intermediate (~1.8 m DTG) and dry (~2.3 m DTG) and observation intervals 2013–2020 (a), 2016–2020 (b) and the “combined rates” (c). *Q. robur* had no recruits across all groundwater classes and census intervals and is omitted from the figure. *C. betulus* had no (2016–2020) or very low (0.062 ha/year, combined rates) in the dry groundwater class and was omitted for improved readability.

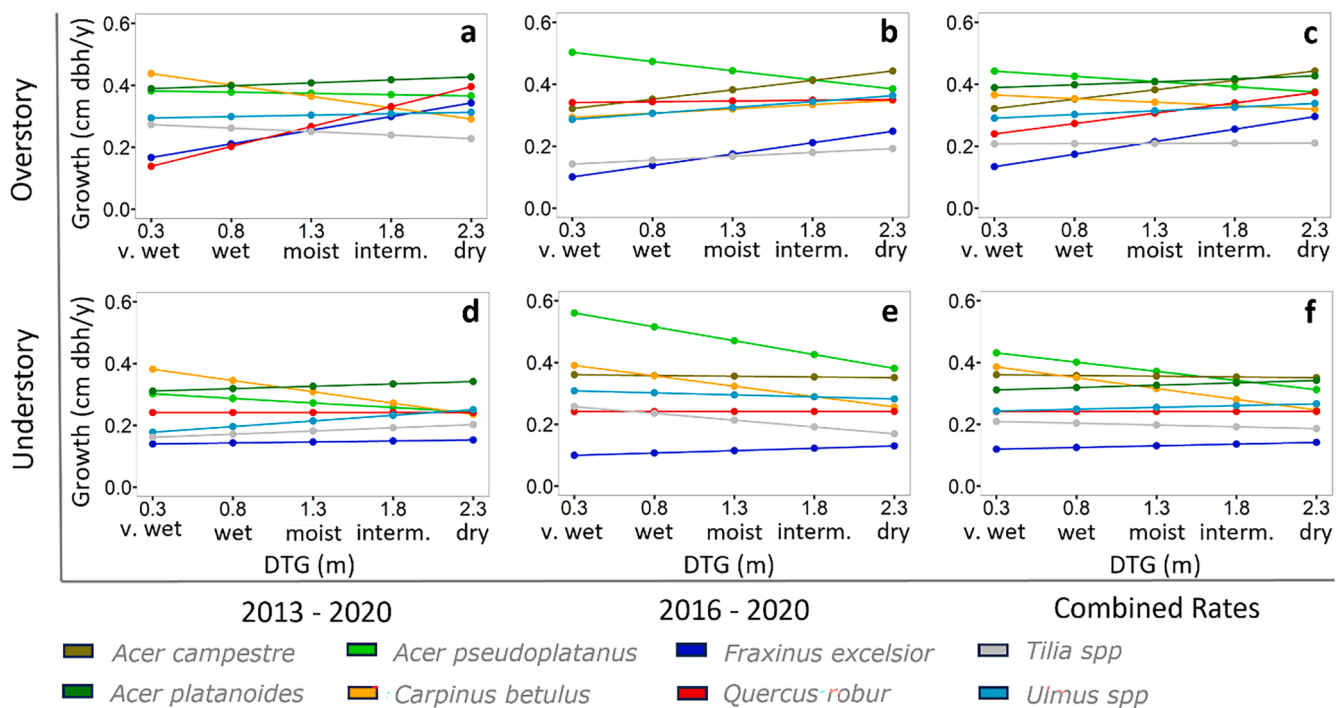
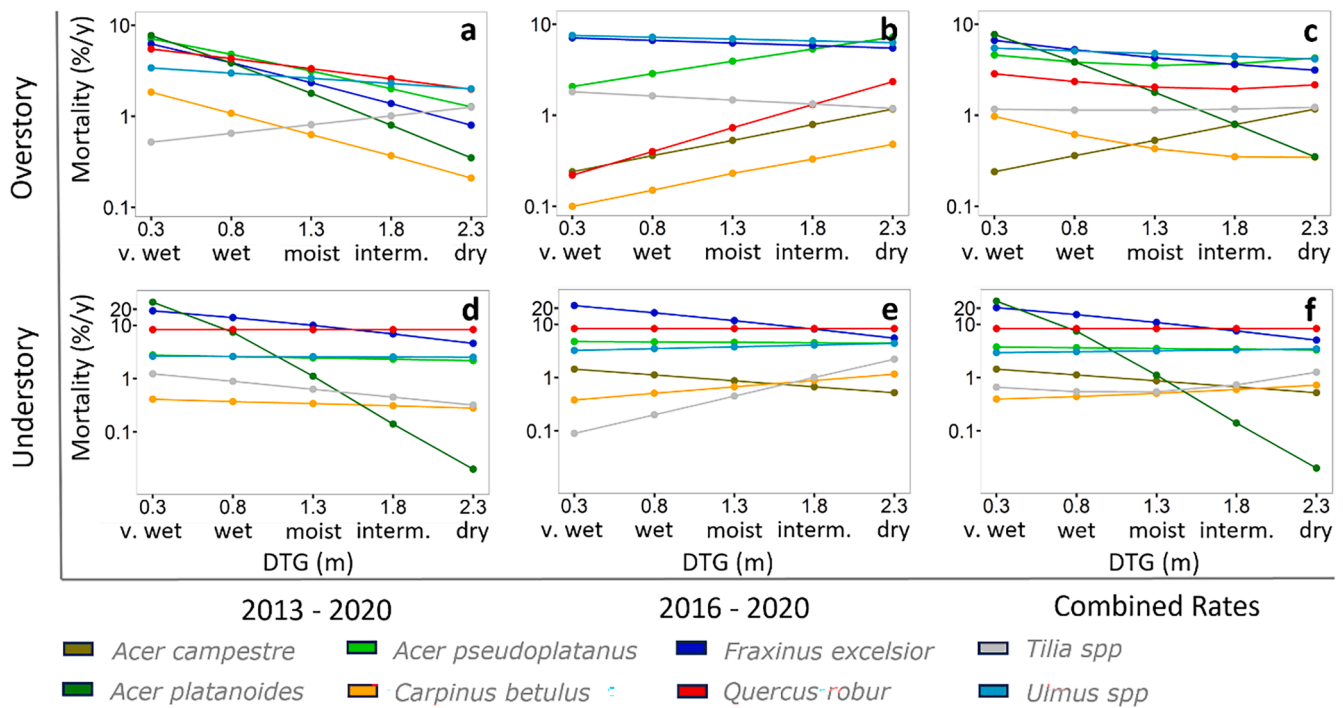


Fig. 3. Annual diameter growth rates for eight focal species in the overstorey (a,b,c) and understorey (d,e,f) in response to distance to groundwater (DTG) for the census interval 2013–2020 (a,d), 2016–2020 (b,e), and the combined rates (c,f). *A. campestre* is excluded in the interval 2013–2020 (a,d), *A. platanoides* is excluded in the interval 2016–2020 (b,e). *Q. robur* understorey growth is determined as average understorey growth over both census intervals independent of DTG (d-f).

overstorey basal area for the currently dominant tree species—*Q. robur*, *F. excelsior*, and *A. pseudoplatanus*—in most scenarios (Fig. 5). Exceptions are *Q. robur* in moist and intermediate sites using demographic rates from 2016 to 2020 (Fig. 5d,e) and *F. excelsior* and *A. pseudoplatanus* in dry sites using demographic rates from 2013 to 2020 (Fig. 5c). *A. campestre*, *A. platanoides*, and *C. betulus* were generally projected to increase in basal area. In scenarios where *A. campestre* was present (2016–2020, combined rates), it was projected to become dominant in moist sites (Fig. 5d,g). In intermediate sites, *C. betulus* was projected to become dominant (Fig. 5b,e,h). In dry sites, *A. platanoides* was projected to become dominant when combined demographic rates were used (Fig. 5j). The basal area of *Ulmus* spp. and *Tilia* spp. remained relatively constant, except for an increase in *Tilia* spp. basal area in moist sites using demographic rates from 2013 to 2020 (Fig. 5a). Projections of understorey basal area are available in Fig. S3. The sensitivity analysis

showed that late-successional dominance was most sensitive to overstorey mortality rate and overstorey growth rate (Fig. S5). Understorey performance and recruitment rate had a comparably minor effect on  $D^*$ . Under a raised groundwater level, the model also projected substantial declines in the main tree species—*Q. robur*, *F. excelsior*, and *A. pseudoplatanus*—in all sites regardless of their initial DTG. *A. campestre* was projected to become dominant in all scenarios when the groundwater was raised by 1 m (Fig. 6c,f,j) as well as in initially dry and moist sites when the groundwater was raised by 0.5 m (Fig. 6b,h). *C. betulus* also increased in basal area in all scenarios and became dominant at intermediate sites when the groundwater was raised by 0.5 m (Fig. 6e). *Ulmus* spp. and *Tilia* spp. were only slightly affected by a raise of the groundwater level in all scenarios. Projections of understorey basal area are available in Fig. S4.



**Fig. 4.** Annual mortality rates for eight focal species in the overstory (a,b,c) and understory (d,e,f) in response to distance to groundwater (DTG) for the census interval 2013–2020 (a,d), 2016–2020 (b,e) and the combined rates (c,f). *A. campestre* is excluded in the interval 2013–2020 (a,d), *A. platanoides* is excluded in the interval 2016–2020 (b, e), and *Q. robur* understory mortality is determined as average understory mortality over both census intervals independent of DTG (d-f).

#### 4. Discussion

We evaluated the potential of a planned raise of the groundwater level in the Leipzig Floodplain Forest (LFF) to conserve the typical floodplain species with high biodiversity value, specifically *Q. robur* and *F. excelsior*. To address this question, we first quantified recruitment, growth, and mortality rates across a gradient of the distance to groundwater (DTG) in two census periods and then used a demographic forest model to project long-term consequences for the species composition of the forest. The results show that the different species varied in the response of their demographic rates to DTG. Under current groundwater conditions, the model projected a substantial decline of the typical floodplain species over 100 years. Likewise, a raise of the groundwater level alone, was not projected to increase the dominance of *Q. robur* and *F. excelsior*. However, the less flood-tolerant *A. platanoides* was projected to be inhibited by a raise of the groundwater level. Since the demographic rates are associated with several uncertainties, the model projections should be interpreted as an exploration of potential consequences of currently observed spatio-temporal variation in demographic rates on the long-term species composition, rather than as predictions.

##### 4.1. Changes in species composition under current groundwater conditions

Under current conditions and with no alteration of the groundwater level, the high-biodiversity value species *Q. robur* and *F. excelsior* are likely to substantially decline in the coming decades. The decline of *Q. robur* from the overstory is unsurprising, as its recruitment rate is zero under all conditions and there are very few trees in the understory that could grow into the overstory. Even though understory demographic rates for *Q. robur* are uncertain due to its low abundance, it is reasonable for this light-demanding species to expect a high understory mortality rate (Boyce et al., 2025). The lack of recruitment shows that under current hydrological conditions, such as the lack of floods that create open spaces and deposit mineral soil, and the strong competition by

abundant shade-tolerant *Acer* regeneration, *Q. robur* is not able to successfully establish (Engelmann et al., 2019; Wirth et al. 2019). Indeed, it is anticipated that the majority of *Q. robur* individuals in the forest are planted and not the result of natural regeneration (Engelmann et al., 2019). The phenomenon of a lack of *Q. robur* regeneration is also observed in other hardwood floodplain forests across Central Europe (Kühne and Bartsch, 2006; Reif et al., 2016; Härdtle et al., 2020).

*F. excelsior* is also projected to substantially decline in most scenarios. This is because next to low recruitment rates, a fungal pathogen introduced from Asia (*Hymenoscyphus fraxineus* T. KOWALSKI) has initially been verified in the LFF in 2010. It infects *F. excelsior* and results in the so-called “ash-dieback” (Engelmann et al., 2019; Erfmeier et al., 2019). In the plots of the “Lebendige Luppe” Project, 71% and 86% of *F. excelsior* individuals showed intermediate to severe damage symptoms in 2017 and 2020, respectively (Engelmann et al., 2019; Wirth et al. 2021). The only scenario where *F. excelsior* did not decline was the one using demographic rates from 2013 to 2020 at dry sites. This is partially explained by the fact that the 2013–2020 data does not incorporate the significant increase in ash dieback in the very last years of the census interval as prominently in the mortality rates as the data from 2016 to 2020. Moreover, in the census interval 2016–2020, despite the extreme heatwave in 2018 and 2019, the mortality rate of *F. excelsior* was elevated in wet areas. This pattern may be attributed to the pathogen’s pronounced impact in wet sites (Marçais et al., 2016; Erfmeier et al., 2019; Henkel et al., 2024). Indeed, the future of *F. excelsior* in the forest remains uncertain, given that only 1–5% of all individuals seem to exhibit immunity to the pathogen (McKinney et al., 2014).

The situation is similar for *A. pseudoplatanus*. It is projected to decline in most scenarios, because of its high mortality rates caused by sooty bark disease, although it had been increasing in abundance and basal area during the past decades (Gläser, 2005; Gutte, 2011; Engelmann et al., 2022; Henkel et al., 2024). “Sooty bark disease” is caused by a fungal pathogen (*Cryptostroma corticale* ELLIS & EVERH.) and often leads to rapid tree mortality (Bork, 2018; Wirth et al., 2021). In the LFF, increased numbers of infections were recorded in 2018 (Seele-Dilbat et al., 2022). The pathogen thrives in conditions of drought and heat

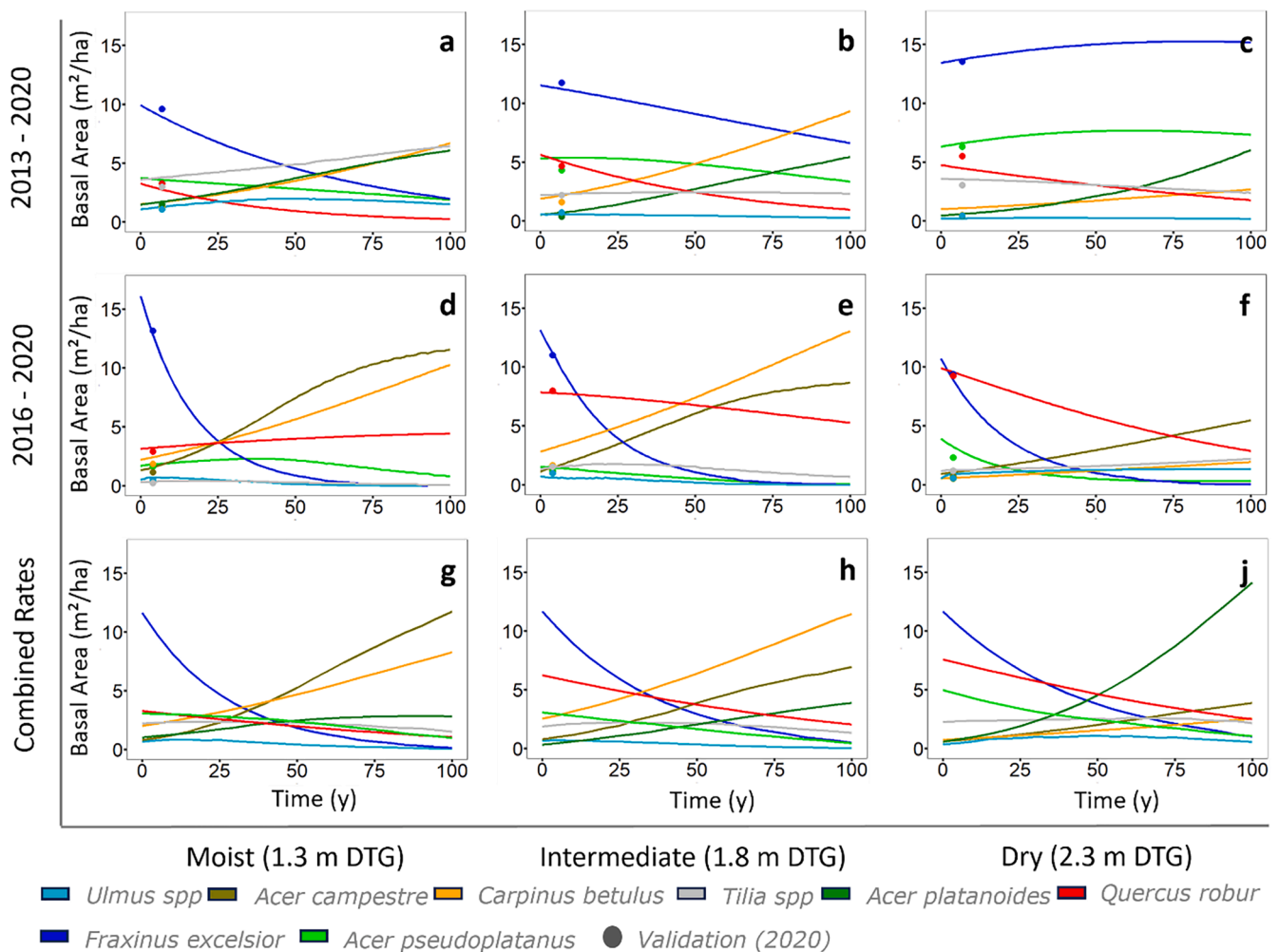


Fig. 5. Projected basal area ( $\text{m}^2/\text{ha}$ ) of eight focal species in the overstorey under current groundwater conditions. Scenarios (a,b,c) use 2013–2020 demographic rates and initial states from 2013 in three groundwater classes and exclude *A. platanoides*. Dots indicate species basal area in 2020 for plots initially measured in 2013. Scenarios (d,e,f) use 2016–2020 demographic rates and initial states from 2016 in three groundwater classes and exclude *A. campestre*. Dots indicate species basal area in 2020 for plots initially measured in 2016. Scenarios (g,h,i) use combined rates and initial states from 2020 in three groundwater classes.

stress in host trees (Bork, 2018). In 2020, 20.1% of sampled *A. pseudoplatanus* individuals had died within a year, and an additional 34.3% exhibited damage symptoms (Wirth et al., 2021). The only scenarios, where *A. pseudoplatanus* did not decline is using demographic rates from 2013 to 2020 at intermediate and dry sites. Again, this is because the longer time interval dilutes the effect of the recent increase in mortality due to sooty bark disease. However, a regeneration inventory (<5 cm dbh, >50 cm height) on the "Lebendige Luppe" plots showed that the relative abundance of *A. pseudoplatanus* accounted for almost 60% of the regeneration in 2022, with an increasing trend (unpublished data). Thus, *A. pseudoplatanus* regeneration is likely to benefit from increased light availability caused by ash dieback. Accordingly, the decline of this species could be weaker than predicted by the model if increasing numbers of saplings <5 cm dbh translate into increasing recruitment rates >5 cm dbh in the coming years.

Under current conditions, three species are projected to increase in basal area in the future. *A. campestre* is projected to become dominant in moist sites, *C. betulus* in intermediate sites, and *A. platanoides* in dry sites when using combined demographic rates. For these species, very low mortality rates were observed during the census intervals. In the census interval 2016–2020, *C. betulus* had a calculated mortality rate of 0.12% per year in moist sites, which is somewhat unrealistic given its average life expectancy of 100 to 150 years (Mayer, 1992; Türk, 1996). Because of the lower abundance of *C. betulus* in moist sites in this census interval

(cf. Tab. S3) and hence larger uncertainty of mortality rates, these projections have to be taken cautiously. Similarly, a low mortality rate is observed for *A. platanoides* in the understorey in dry sites from 2013 to 2020. This, however, may be a realistic estimate, given its high shade tolerance (Engelmann et al., 2019).

It may also be realistic that *A. campestre* will be more successful at moister sites than *A. platanoides* because of its higher flood tolerance (Niinemets and Valladares, 2006; Weißbrod et al., 2014; Kölling et al., 2015). However, the strong increase of *A. campestre* in moist sites predicted by the model contradicts forest inventory surveys, in which the relative dominance of *A. campestre* in the overstorey only modestly increased from 0.5% in the first to 0.6% in the second inventory (Henkel et al., 2024). Moreover, in the southern part of the study area, *A. campestre* has a very low abundance. This species migrates into the forest from the northwest (Gutte, 2011), and it will take time for *A. campestre* to further migrate to the south. This suggests that the increase of *A. campestre* could be overestimated by the model.

The relatively low basal area of *Ulmus* spp. and *Tilia* spp. is projected to remain relatively stable in most scenarios. For *Ulmus* spp., this stability is likely attributed to Dutch elm disease, which infects *Ulmus* trees when they reach an age of around 15–20 years (5–9 m in height, ca. 10 cm dbh, Clarkson and Coleman, 2022). Dutch elm disease has since the 1960s been the main driver for the disappearance of *Ulmus* spp. from the overstorey in the Leipzig Floodplain Forest (Engelmann et al., 2019,

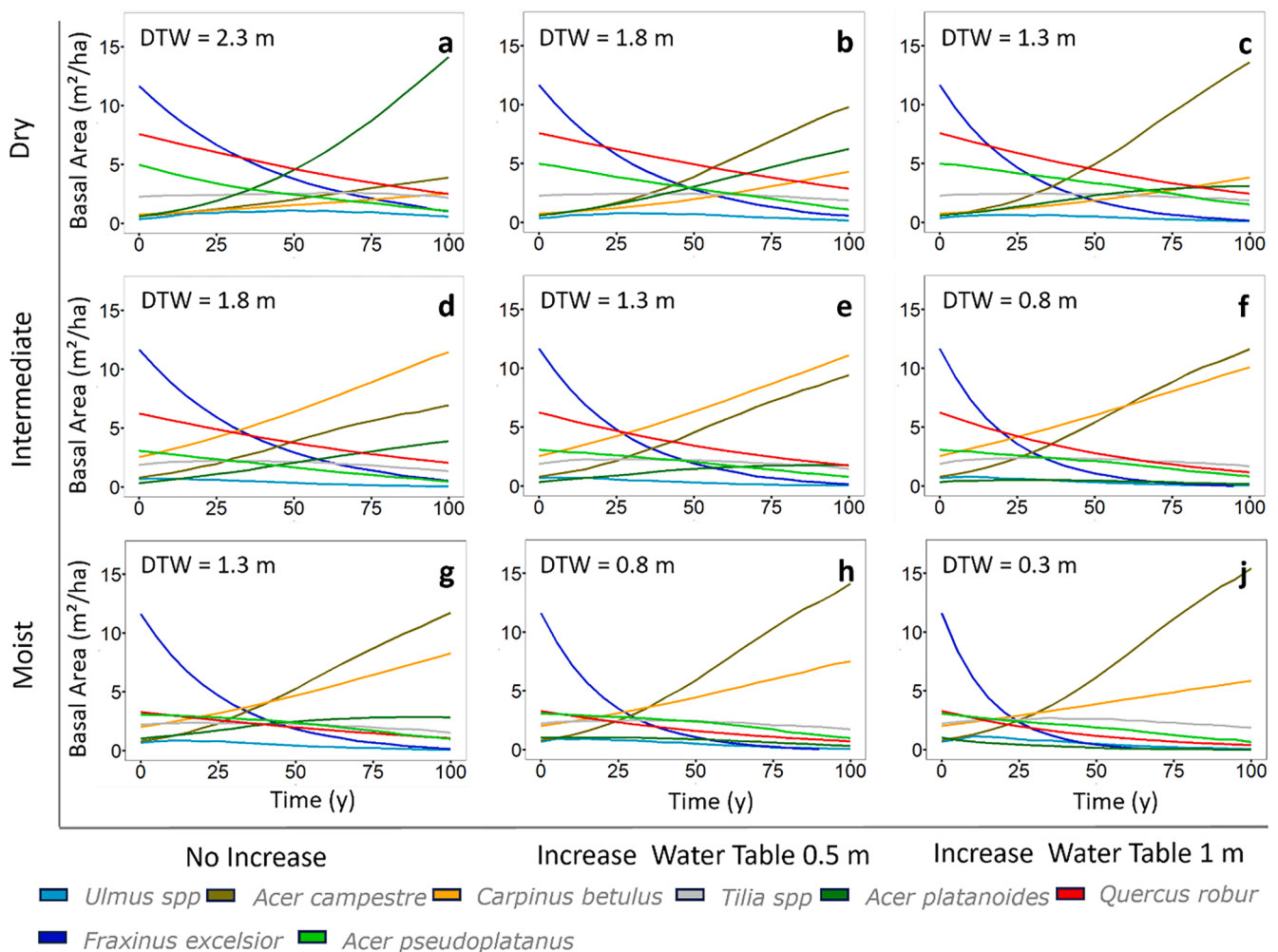


Fig. 6. Projected basal area ( $\text{m}^2/\text{ha}$ ) of eight focal species in the overstorey using combined rates in three groundwater classes under current groundwater levels (a,d,g), a raise of the groundwater level by 0.5 m (b,e,h), and by 1 m (c,f,i).

2022; Wirth et al., 2021).

The projected changes in forest composition in general align with short-term observations in the study site. We attribute the slight differences between the model predictions and observed species-specific basal area in 2020 to the differences in how demographic rates and basal area were calculated. While recruitment rates and basal area were calculated using plot-level assignments to discrete groundwater classes, growth and mortality rates were predicted based on the distance to groundwater assigned to individual trees. Model projections also generally align with expectations on the potential transformation of the LFF based on empirical observations, namely the expected decline of *Q. robur* and *F. excelsior* and the increasing dominance of *Acer* spp. (Engelmann et al., 2019; Wirth et al., 2020).

#### 4.2. Changes in species composition under raised groundwater levels

To project the species composition in the LFF under raised groundwater levels, we used the combined demographic rates, which encompass all eight species, the entire observation period, and the entire spatial distribution of survey plots. Model projections show that a raise of the groundwater level would not impede or slow down the decline of the high-biodiversity value tree species *Q. robur* and *F. excelsior*. This is because the response of mortality to groundwater level differed between the two census intervals and disappeared in the combined demographic rates. Additionally, the recruitment rate of *Q. robur* was zero independent of the groundwater level. While the future of *F. excelsior* in the LFF

is uncertain due to the ash dieback, *Q. robur* regeneration can be promoted by forest management. Currently, oak is successfully planted in femels (Gläser and Schmidt, 2007; Sickert, 2007; Boyce et al., 2025), i.e. in small clearings or gaps in the forest canopy that ensure sufficient light availability for successful oak regeneration (Joyce and Gardiner, 1986; Sevillano et al., 2016; Mölder et al., 2019).

According to model projections, *A. campestre* would replace *A. platanoides* in dry sites and, in general, the higher the groundwater level, the higher the projected dominance of *A. campestre*. This is because the mortality rates for *A. campestre* in the overstorey declined to very low levels at the highest groundwater levels. However, this relationship is derived from only very few mortality events of *A. campestre* during the census interval and consequently associated with large uncertainty.

It is important to note that a raise of groundwater level is not an isolated intervention but rather a co-benefit of a comprehensive restoration initiative. This initiative includes raising riverbeds, reactivating and integrating antiquated watercourses, dismantling or perforating dikes, and ensuring overall permeability along streams (Wirth et al., 2020). These measures should, in conjunction with a raised groundwater level, ultimately increase the frequency of smaller and medium flood events across the floodplain (Engelmann et al., 2019; Wirth et al., 2020). While there are studies on the flood tolerance of the focal species (Dister, 1988; Späth, 1988, 2002; Niinemets and Valladares, 2006; Weißbrod et al., 2014), site-specific information on its impacts on demographic rates is currently unavailable and could not be incorporated



in this study. Long floods in the vegetation period could notably reduce the abundance of *A. platanoides* (Späth, 1988, 2002; Weißbrod et al., 2014), *A. pseudoplatanus* (Späth, 1988, 2002; Macher, 2009), and other seedlings (Kramer et al., 2008). This could benefit the regeneration of *Q. robur* through decreased competition. Likewise, the deposition of substrate due to substrate dynamics after intense floods could also benefit *Q. robur* regeneration (Reif et al., 2016). However, in the LFF the upstream weir "Elsterwehr" retains a significant portion of the substrate. Even though our results do not fully capture potential effects of a comprehensive hydrological restoration, they offer insights into one of its components, specifically the raise of groundwater levels.

#### 4.3. Limitations

Several sources of uncertainty were already mentioned in the previous sections, including the two different census intervals (2013–2020 versus 2016–2020), that differentially reflect the severity of new diseases and the low abundance of some species in one or both canopy layers. Moreover, the canopy layer assignment using the allometric crown area estimation may have led to an unrealistically high number of *Ulmus* spp. and *A. campestre* in the overstory. Studies using the five discrete dominance classes ("Kraftsche-Klassen" method; Henkel et al., 2024) or tree heights (Engelmann et al., 2019, 2022) for canopy layer assignment have shown that the abundance of *Ulmus* spp. and *A. campestre* in the overstory is low.

Another factor that affected the two census intervals differently was an extreme flood event in June 2013 that temporarily flooded 44 plots for 5 to 8 days with a maximum flood height of 1.92 m (Scholz et al., 2022; Seele-Dilbat et al., 2022). Floods during the vegetation period have species-specific impacts on demographic rates (Kramer et al., 2008; Weißbrod et al., 2014; Heklau et al., 2019). For instance, a severe flood in the Rhine floodplain forest was linked to a notable increase in mortality for *A. platanoides*, *A. pseudoplatanus*, *T. cordata*, *C. betulus*, and *F. excelsior* (Kramer et al., 2008). The plots censused initially in 2013 do more fully include the effects of the flood than the plots censused in 2016 because trees that were censused in 2013 might have died during subsequent years and contributed to higher mortality rates in moist sites in the census interval 2013–2020. However, in the plots initially censused in 2016, many of these trees might already have died and not entered the census, and thus not contributed to higher records of mortality in the census interval 2016–2020. This discrepancy can potentially explain the higher mortality and lower growth rates observed in moist sites in 2013–2020 as compared to 2016–2020.

Both census intervals also encompassed two consecutive extreme drought years in 2018 and 2019, that resulted in reduced growth rates and physiological stress responses in 2019 for *Q. robur*, *F. excelsior*, and *A. pseudoplatanus* (Schnabel et al., 2022). However, their impact is more pronounced in the annual rates derived from 2016 to 2020 due to the shorter observation time. The sensitivity analysis showed that uncertainties in overstory performance (i.e. growth and mortality) have a larger impact on model projections.

In sum, model projections should be interpreted as an exploration of model results across observed ranges of demographic rates for specific conditions in time and space, rather than as predictions of changes in species composition. This is especially important in the face of large uncertainty regarding the effects of climate change and pathogen dynamics on demographic rates of the tree species in the future, which are not incorporated in this study. However, some results were robust across the scenarios and illustrate likely future changes, such as the decline of *Q. robur* and *F. excelsior* and the increase in dominance of *A. campestre* and *C. betulus*.

#### 5. Conclusions

Our results indicate that the species composition of the Leipzig Floodplain Forest will likely change in the future. *Q. robur*, *F. excelsior*,

and *A. pseudoplatanus* are projected to decline. For *Q. robur* this is mainly due to the lack of recruitment caused by strong competition, for *F. excelsior* and *A. pseudoplatanus* this is mainly due to the high prevalence of ash dieback and sooty bark disease during the last years. Conversely, *A. campestre*, *C. betulus*, and in dry sites *A. platanoides* are projected to increase in basal area. A raise of the groundwater level alone is unlikely to prevent the decline of *Q. robur* and *F. excelsior*, but favors *A. campestre* and *C. betulus*. However, it may inhibit the regeneration of less flood-tolerant species, such as *A. platanoides*. This means that conservation strategies aiming at maintaining the characteristic floodplain tree species and their associated biodiversity should not only rely on the raise of the groundwater level. Even though the degree to which more frequent floods, climate change, or pathogens will affect the species composition in the Leipzig Floodplain Forest in the future remains uncertain, this study illustrates how detailed forest inventory data across environmental gradients can enable the application of ecological models to support conservation planning.

#### Declaration of generative AI in scientific writing

No artificial intelligence tools, either generative or corrective, were used in conducting this work or writing this paper.

#### CRediT authorship contribution statement

**Lucian Elles:** Writing – original draft, Visualization, Investigation, Formal analysis. **Jack Boyce:** Writing – review & editing, Formal analysis. **Stefanie Henkel:** Writing – review & editing, Data curation. **Hans D. Kasperidus:** Writing – review & editing, Data curation. **Mathias Scholz:** Writing – review & editing, Data curation, Conceptualization. **Markus E. Schorn:** Writing – review & editing, Resources. **Michael Vieweg:** Writing – review & editing, Resources, Data curation. **Christian Wirth:** Writing – review & editing, Data curation, Conceptualization. **Nadja Rüger:** Writing – review & editing, Supervision, Methodology, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgements

The authors would like to thank the colleagues from the "Lebendige Luppe" project for collecting and managing the forest survey data and helpful advice (especially Rolf Engelmann, Georg Rieland, and Carolin Seele-Dilbat), Andreas Sickert and Andreas Padberg for insightful discussions, and Adam Clark for co-supervising the master's thesis. We are grateful for constructive comments from one anonymous reviewer.

NR was supported by the Senior Scientist Programme of the German Centre for Integrative Biodiversity Research (iDiv) Halle- Jena-Leipzig (DFG, FZT 118). The "Lebendige Luppe" project was funded by the German Federal Agency for Nature Conservation with funds from the Federal Ministry for the Environment, Nature Conservation and Nuclear Safety as part of the Federal Biological Diversity Program. The State of Saxony supported the project through the nature conservation fund of the Saxon State Foundation for Nature and the Environment. Further information can be found on the project homepage [www.Lebendige-Luppe.de](http://www.Lebendige-Luppe.de).

#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2024.110996](https://doi.org/10.1016/j.ecolmodel.2024.110996).

## Data availability

The model code, parameters, initial states, model outputs etc. are available at: [https://github.com/lucian-elles/Elles\\_et\\_al\\_2024\\_Supporting\\_conservation\\_planning\\_in\\_a\\_national\\_biodiversity\\_hotspot](https://github.com/lucian-elles/Elles_et_al_2024_Supporting_conservation_planning_in_a_national_biodiversity_hotspot)

## References

- Bork, K., 2018. Rußrindkrankheit an Ahorn – Erstfund in Bayern. *AFZ – Der Wald* 20, 40–41.
- Boyce, J., Elles, L., Henkel, S., Kasperidus, H.D., Scholz, M., Schorn, M.E., Sickert, A., Padberg, A., Vieweg, M., Rüger, N., 2025. How can oak regeneration in the Leipzig Floodplain Forest be effectively supported by femel plantations? Application of a demographic forest model. *Ecol. Modell.* 499, 110920.
- Clarkson, R., Coleman, M., 2022. Propagating healthy mature elms that have survived in areas severely impacted by Dutch elm disease: a scoping study for a wych elm project in Scotland. *Royal Botanic Garden Edinburgh*.
- Crow, T.R., Baker, M.E., Barnes, B.V., 2000. Diversity in Riparian Landscapes. In: Verry, E.S., Hornbeck, J.W., Dollhoff, C.A. (Eds.), *Riparian Management of Forests in the Continental Eastern United States*. Lewis Publishers, pp. 43–66. <https://www.gbv.de/dms/goettingen/306062534.pdf>.
- Dister, E., 1988. Zur Hochwassertoleranz von Auwaldbäumen an lehmigen Standorten. *Verhandlung Der Gesellschaft Für Ökologie* 10, 325–336.
- Ellison, D., Morris, C.E., Locatelli, B., Sheil, D., Cohen, J., Murdiyasar, D., Gutierrez, V., van Noordwijk, M., Creed, I.F., Pokorny, J., Gaveau, D., Spracklen, D.V., Tobella, A. B., Ilsted, U., Teuling, A.J., Gebrehiwot, S.G., Sands, D.C., Muys, B., Verbist, B., Springgay, E., Sugandi, Y., Sullivan, C.A., 2017. Trees, forests and water: cool insights for a hot world. *Global Environ. Change* 43, 51–61. <https://doi.org/10.1016/j.gloenvcha.2017.01.002>.
- Engelmann, R., Haack, N., Henle, K., Kasperidus, H., Nissen, S., Schlegel, M., Scholz, M., Seele-Dilbat, C., Wirth, C., 2019. Reiner Prozessschutz gefährdet Artenvielfalt im Leipziger Auwald. *UFZ Discussion Paper* 8/2019. Helmholtz-Zentrum für Umweltforschung (UFZ). (In German). Retrieved from <https://www.econstor.eu/bitstream/10419/209624/1/1685446353.pdf>.
- Engelmann, R., Seele-Dilbat, C., Hartmann, T., Pruschitzki, U., Kasperidus, H., Scholz, M., Wirth, C., 2022. Der Gehölzbestand des Stieleichen-Ulmen-Hartholzaeuwalds (*Quercus-Ulmetum minoris* ISSLER 1942) im Projektgebiet Lebendige Luppe in der Elster-Luppe-Aue bei Leipzig. *Die Elster-Luppe-Aue – eine wertvolle Auenlandschaft: Ergebnisse der wissenschaftlichen Begleitung aus dem Projekt Lebendige Luppe (UFZ-Bericht 2/2022)* 115–132. [10.57699/RXX9-ZH02](https://doi.org/10.57699/RXX9-ZH02).
- Erfmeier, A., Haldan, K.L., Beckmann, L.-M., Behrens, M., Rotert, J., Schrautzer, J., 2019. Ash dieback and its impact in near-natural forest remnants - A plant community-based inventory. *Front. Plant Sci.* 10, 658. <https://doi.org/10.3389/fpls.2019.00658>.
- Gee, H.K., King, S.L., Keim, R.F., 2014. Tree growth and recruitment in a leveed floodplain forest in the Mississippi River Alluvial Valley, USA. *For. Ecol. Manage.* 334, 85–95. <https://doi.org/10.1016/j.foreco.2014.08.024>.
- Gläser, J. (2005). *Untersuchungen zur historischen Entwicklung und Vegetation mitteldeutscher Auenwälder* (PhD Dissertation).
- Gläser, J., Schmidt, P.A., 2007. The historical development of the composition of tree species in floodplain forests - Demonstrated on the example floodplain forests in Leipzig. *Allgemeine Forst- und Jagdzeitung* 178, 90–97.
- Gregory, S.V., Swanson, F.J., McKee, W.A., Cummins, K.W., 1991. An ecosystem perspective of riparian zones. *Bioscience* 41, 540–551. <https://doi.org/10.2307/1311607>.
- Gutte, P., 2011. *Das Quercus-Ulmetum minoris Issler 1942, der Stieleichen-Ulmen-Hartholzwald, in der Elster-Luppe-Aue bei Leipzig*. *Mauritiana* 22, 213–242.
- Haack, N., Bourges, P.A.V., Grimm-Seyfarth, A., Schlegel, M., Wirth, C., Bernhard, D., Pereira, H.M., 2022. Response of common and rare beetle species to tree species and vertical stratification in a floodplain forest. *Insects* 13, 161. <https://doi.org/10.3390/insects13020161>.
- Haack, N., Grimm-Seyfarth, A., Schlegel, M., Wirth, C., Bernhard, D., Brunk, I., Henle, K., 2021. Patterns of richness across forest beetle communities – A methodological comparison of observed and estimated species numbers. *Ecol. Evol.* 11, 626–635. <https://doi.org/10.1002/ece3.7093>.
- Hansen, A.J., Garman, S.L., Weigand, J.F., Urban, D.L., McComb, W.C., Raphael, M.G., 1995. Alternative silvicultural regimes in the Pacific Northwest: simulations of ecological and economic effects. *Ecol. Appl.* 5, 535–554. <https://doi.org/10.2307/1941965>.
- Härdtke, W., Bergmeier, E., Fichtner, A., Heinken, T., Hölzel, N., Remy, D., Schneider, S., Schwabe, A., Tischew, S., Dierschke, H., 2020. Pflanzengesellschaft des Jahres 2021: Hartholz-Auenwald (*Ficario-Ulmetum*). *Tuexenia* 40, 373–399. <https://doi.org/10.14471/2020.40.007>.
- Havrdová, A., Douda, J., Doudová, J., 2023. Threats, biodiversity drivers and restoration in temperate floodplain forests related to spatial scales. *Sci. Total Environ.* 854, 158743. <https://doi.org/10.1016/j.scitotenv.2022.158743>.
- Heklau, H., Jetschke, G., Bruelheide, H., Seidler, G., Haider, S., 2019. Species-specific responses of wood growth to flooding and climate in floodplain forests in Central Germany. *IForest* 12, 226–236. <https://doi.org/10.3832/ifer02845-012>.
- Henkel, S., Richter, R., Andrzejek, K., Mundry, R., Dontschev, M., Engelmann, R., Hartmann, T., Hecht, C., Kasperidus, H.D., Rieland, G., Scholz, M., Seele-Dilbat, C., Vieweg, M., Wirth, C., 2024. Floodplain forests under stress: how ash dieback and hydrology affect tree growth patterns under climate change. Preprint Research Square. [10.21203/rs.3.rs-4676274/v1](https://doi.org/10.21203/rs.3.rs-4676274/v1).
- Holzwarth, F., Rüger, N., Wirth, C., 2015. Taking a closer look: disentangling effects of functional diversity on ecosystem functions with a trait-based model across hierarchy and time. *R. Soc. Open. Sci.* 2, 140541. <https://doi.org/10.1098/rsos.140541>.
- Hughes, F.M.R., Del Tánago, M.G., Mountford, J.O., 2012. Restoring floodplain forests in Europe. J. Stanturf, P. Madsen, D. Lamb. In: *World Forests. A Goal-Oriented Approach to Forest Landscape Restoration*, Vol. 16. Springer, Netherlands, pp. 393–422. [https://doi.org/10.1007/978-94-007-5338-9\\_15](https://doi.org/10.1007/978-94-007-5338-9_15).
- Joyce, P.M., Gardiner, J.J., 1986. The Management of oak in Germany: a silvicultural Note. *Irish Forestry* 43, 56–65.
- Kirsten, F., Herkelrath-Bleyl, A., Krüger, A., Heinrich, J., 2022. Entstehung und Eigenschaften der Böden und Sedimente in der Elster-Luppe-Aue. *Die Elster-Luppe-Aue – eine wertvolle Auenlandschaft: Ergebnisse der wissenschaftlichen Begleitung aus dem Projekt Lebendige Luppe (UFZ-Bericht 2/2022)*, pp. 43–68. [10.57699/RXX9-ZH02](https://doi.org/10.57699/RXX9-ZH02).
- Klimo, E., Hager, H., 2001. The Floodplain Forests in Europe: Current situation and Perspectives. 10. European Forest Institute Research Report, Brill, Leiden, Boston, Köln, p. 267.
- Kölling, C., Taeger, S., Mellert, K.H., Falk, W., 2015. Der Feldahorn als Alternative im Waldumbau: Klima- und Bodenansprüche. *LWF Wissen* 77, 22–29.
- Kramer, K., Vreugdenhil, S.J., van der Werf, D.C., 2008. Effects of flooding on the recruitment, damage and mortality of riparian tree species: a field and simulation study on the Rhine floodplain. *For. Ecol. Manage.* 255, 3893–3903. <https://doi.org/10.1016/j.foreco.2008.03.044>.
- Kühne, C., Bartsch, N., 2006. Verjüngung der Stieleiche am Oberrhein zwischen Karlsruhe und Speyer. *Waldschutzgebiete Baden-Württemberg* 10, 75–84.
- Leuschner, C., Ellenberg, H., 2017. Woody Vegetation of Floodplains and Swamps. In: Leuschner, C., Ellenberg, H. (Eds.), *Ecology of Central European Forests*. Springer International Publishing, pp. 633–728. [https://doi.org/10.1007/978-3-319-43042-3\\_9](https://doi.org/10.1007/978-3-319-43042-3_9).
- Macher, C., 2009. Überflutungstoleranz des Bergahorns – ein Überblick zum derzeitigen Kenntnisstand. *LWF Wissen* 63, 33–35.
- Marçais, B., Husson, C., Godart, L., Caël, O., 2016. Influence of site and stand factors on *Hymenoscyphus fraxineus*-induced basal lesions. *Plant Pathol.* 65, 1452–1461. <https://doi.org/10.1111/ppa.12542>.
- Mayer, H., 1992. *Waldbau auf soziologisch-ökologischer Grundlage*. Gustav Fischer Verlag, p. 522.
- McKinney, L.V., Nielsen, L.R., Collinge, D.B., Thomsen, I.M., Hansen, J.K., Kjær, E.D., 2014. The ash dieback crisis: genetic variation in resistance can prove a long-term solution. *Plant Pathol.* 63, 485–499. <https://doi.org/10.1111/ppa.12196>.
- Mikac, S., Žmegač, A., Trlin, D., Paulič, V., Oršanić, M., Anič, I., 2018. Drought-induced shift in tree response to climate in floodplain forests of Southeastern Europe. *Sci. Rep.* 8, 16495. <https://doi.org/10.1038/s41598-018-34875-w>.
- Mölder, A., Meyer, P., Nagel, R.-V., 2019. Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: an overview. *For. Ecol. Manage.* 437, 324–339. <https://doi.org/10.1016/j.foreco.2019.01.006>.
- Niinemetts, Ü., Valladares, F., 2006. Tolerance to shade, drought and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547. [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2).
- Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeier, S., Esipova, E., 2017. The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. *Sci. Adv.* e1600821 <https://doi.org/10.1126/sciadv.1600821>, 3.
- Pramova, E., Locatelli, B., Djoudi, H., Somorin, O.A., 2012. Forests and trees for social adaptation to climate variability and change. *WIREs Clim. Change* 3, 581–596. <https://doi.org/10.1002/wcc.195>.
- Purves, D.W., Lichstein, J.W., Strigul, N., Pacala, S.W., 2008. Predicting and understanding forest dynamics using a simple tractable model. *Proc. Natl. Acad. Sci. U.S.A.* 105, 17018–17022. <https://doi.org/10.1073/pnas.0807754105>.
- R Development Core Team, 2022. R version 4.2.1 R Project for Statistical Computing, Vienna, Austria.
- Reif, A., Baumgärtel, R., Dister, E., Schneider, E., 2016. Zur Natürlichkeit der Stieleiche (*Quercus robur* L.) in Flussauen Mitteleuropas – eine Fallstudie aus dem Naturschutzgebiet „Kühkopf-Knoblochsau“ am hessischen Oberrhein. *Waldökologie, Landschaftsforschung und Naturschutz* 15, 69–92.
- Rieland, G., Scholz, M., Engelmann, R.A., Hartmann, T., Hecht, C., Henkel, S., Kasperidus, H., Pruschitzki, U., Wirth, C., Seele-Dilbat, C., 2024. Tree Inventory Dataset of Floodplain Forest. PANGAEA, Leipzig, Germany. <https://doi.pangaea.de/10.1594/PANGAEA.968663>.
- Riis, T., Kelly-Quinn, M., Aguiar, F.C., Manolaki, P., Bruno, D., Bejarano, M.D., Clerici, N., Fernandes, M.R., Franco, J.C., Pettit, N., Portela, A.P., Tammeorg, O., Tammeorg, P., Rodríguez-González, P.M., Dufour, S., 2020. Global overview of ecosystem services provided by riparian vegetation. *Bioscience* 70, 501–514. <https://doi.org/10.1093/biosci/biaa041>.
- Rüger, N., Condit, R., Dent, D.H., DeWalt, S.J., Hubbell, S.P., Lichstein, J.W., Lopez, O.R., Wirth, C., Farrior, C.E., 2020. Demographic trade-offs predict tropical forest dynamics. *Science* 368, 165–168. <https://doi.org/10.1126/science.aaz4797>.
- Rüger, N., Gutiérrez, Á.G., Kissling, W.D., Armesto, J.J., Huth, A., 2007. Ecological impacts of different harvesting scenarios for temperate evergreen rain forest in southern Chile—A simulation experiment. *For. Ecol. Manage.* 252, 52–66. <https://doi.org/10.1016/j.foreco.2007.06.020>.
- Schnabel, F., Purucker, S., Schmitt, L., Engelmann, R.A., Kahl, A., Richter, R., Seele-Dilbat, C., Skidaresis, G., Wirth, C., 2022. Cumulative growth and stress responses to the 2018–2019 drought in a European floodplain forest. *Glob. Chang. Biol.* 28, 1870–1883. <https://doi.org/10.1111/gcb.16028>.

- Schnitzler, A., Hale, B.W., Alsum, E.M., 2007. Examining native and exotic species diversity in European riparian forests. *Biol. Conserv.* 138, 146–156. <https://doi.org/10.1016/j.biocon.2007.04.010>.
- Scholz, M., Seele-Dilbat, C., Engelmann, R.A., Kasperidus, H.D., Kirsten, F., Herkelrath-Bleyl, A., Vieweg, M., 2022. Das Projekt Lebendige Luppe - Einführung in den Untersuchungsraum Elster-Luppe-Aue. Die Elster-Luppe-Aue – eine wertvolle Auenlandschaft: Ergebnisse der wissenschaftlichen Begleitung aus dem Projekt Lebendige Luppe (UFZ-Bericht 2/2022), pp. 7–20. [10.57699/RXX9-ZH02](https://doi.org/10.57699/RXX9-ZH02).
- Seele-Dilbat, C., Engelmann, R.A., Heinrich, J., Henle, K., Herkelrath-Bleyl, A., Kasperidus, H.D., Krüger, 2022. Untersuchungsdesign der naturwissenschaftlichen Begleitung im Projekt Lebendige Luppe. Die Elster-Luppe-Aue – eine wertvolle Auenlandschaft: Ergebnisse der wissenschaftlichen Begleitung aus dem Projekt Lebendige Luppe (UFZ-Bericht 2/2022), pp. 115–132. [10.57699/RXX9-ZH02](https://doi.org/10.57699/RXX9-ZH02).
- Šenfeldr, M., Horák, P., Kvasnica, J., Šrámek, M., Hornová, H., Maděra, P., 2021. Species-specific effects of groundwater level alteration on climate sensitivity of floodplain trees. *Forests* 12, 1178. <https://doi.org/10.3390/f12091178>.
- Sevillano, I., Short, I., Grant, J., O'Reilly, C., 2016. Effects of light availability on morphology, growth and biomass allocation of *Fagus sylvatica* and *Quercus robur* seedlings. *For. Ecol. Manage.* 374, 11–19. <https://doi.org/10.1016/j.foreco.2016.04.048>.
- Sickert, A., 2007. Forestry management systems applied to Leipzig's Floodplain Forest. *Forest Management Systems and Regeneration of floodplain forest sites*. In: Reviewed proceedings from the international conference in Brno, Czech Republic. Mendel University of Agriculture and Forestry, pp. 61–72. In: <https://palivec.entu.cas.cz/~cizek/LuzniLesKonfera/BRNO%202007%20Proceedings.pdf>.
- Skiadareis, G., Schwarz, J.A., Bauhus, J., 2019. Groundwater extraction in floodplain forests reduces radial growth and increases summer drought sensitivity of pedunculate oak trees (*Quercus robur* L.). *Front. For. Glob. Change* 2, 5. <https://doi.org/10.3389/ffgc.2019.00005>.
- Späth, V., 1988. Zur Hochwassertoleranz von Auwaldbäumen. *Natur und Landschaft* 63, 312–315.
- Späth, V., 2002. Hochwassertoleranz von Bäumen in der Rheinaue. *AFZ – Der Wald* 15, 807–810.
- Strigul, N., Pristinski, D., Purves, D., Dushoff, J., Pacala, S., 2008. Scaling from trees to forests: tractable macroscopic equations for forest dynamics. *Ecol. Monogr.* 78, 523–545. <https://doi.org/10.1890/08-0082.1>.
- Stojanović, D.B., Levanić, T., Matović, B., Orlović, S., 2015. Growth decrease and mortality of oak floodplain forests as a response to change of water regime and climate. *Eur. J. For. Res.* 134, 555–567. <https://doi.org/10.1007/s10342-015-0871-5>.
- Szatniewska, J., Zavadilova, I., Nezval, O., Krejza, J., Petrik, P., Čáter, M., Stojanović, M., 2022. Species-specific growth and transpiration response to changing environmental conditions in floodplain forest. *For. Ecol. Manage.* 516, 120248. <https://doi.org/10.1016/j.foreco.2022.120248>.
- Toraño Caicoya, A., Biber, P., Poschenrieder, W., Schwaiger, F., Pretzsch, H., 2018. Forestry projections for species diversity-oriented management: an example from Central Europe. *Ecol. Process.* 7, 23. <https://doi.org/10.1186/s13717-018-0135-7>.
- Türk, W., 1996. Die Hainbuche in der realen und potentiellen natürlichen Vegetation Mitteleuropas unter besonderer Berücksichtigung Bayerns. In: Schmidt, O. (Ed.), Beiträge zur Hainbuche. *LWF* 12, 17–25.
- Weißbrod, M., Bindner, F., Aas, G., Mosandl, R., 2014. Überflutungstoleranz von Jungpflanzen: wie reagieren Verjüngungspflanzen auf verschiedene Verjüngungspflanzen auf verschiedene Überstauungshöhen? *LWF aktuell* 101, 38–41.
- Wirth, C., Engelmann, R.A., Haack, N., Hartmann, H., Richter, R., Schnabel, F., Scholz, M., Seele-Dilbat, C., 2021. Naturschutz und Klimawandel im Leipziger Auwald. *Biologie in unserer Zeit* 51, 55–65. <https://doi.org/10.11576/BIUZ-4107>.
- Wirth, C., Franke, C., Carmienie, I., Denner, M., Dittmann, V., Homann, K., Rudolf, H., Schmoll, A., Scholz, M., Senft, I., Steuer, P., Wilke, T., Zabožnik, A., 2020. Dynamik als Leitprinzip zur Revitalisierung des Leipziger Auensystems. *UFZ Discussion Papers* 9/2020. Helmholtz-Zentrum für Umweltforschung – UFZ. <https://www.econstor.eu/bitstream/10419/226368/1/1740352300.pdf>.