



Original Articles

The FraDiv experiment: Biodiversity-ecosystem functioning research meets reforestation practice

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ABSTRACT

European ash-rich forest ecosystems are transforming rapidly under the influence of ash dieback, putting many associated species at risk. Forest managers face the urgent challenge to deal with the loss of European ash (*Fraxinus excelsior* L.) as a key tree species to maintain species richness and ecosystem functioning. The project FraDiv^{exp}, located in Schleswig-Holstein, Germany, aims at counteracting detrimental effects of progressive ash decline by testing alternative tree species in a Biodiversity-Ecosystem Functioning (BEF) experiment along a hydrological gradient. Here, we provide insight into how a BEF-approach can be combined with silvicultural management practice to meet the needs for both ecological research and reforestation. At the same time, we present first data on the survival of the planted saplings.

In winter 2019/2020, FraDiv^{exp} was established with autochthonous tree species considered potential substitutes for the functioning of ash. At 12 sites, plantations including *Fraxinus excelsior*, *Acer platanoides* L., *Carpinus betulus* L., *Tilia cordata* Mill. and *Ulmus laevis* Pall. were planted directly underneath the remains of collapsing forest canopies involving all monocultures, and all combinations of 2-, 4- and 5-species mixtures. One year after planting of 25,200 trees, total mortality was at 5 % with *U. laevis* showing lowest mortality while establishment of *A. platanoides* was least successful. In this early phase of FraDiv^{exp} tree mortality was species-specific and driven by initial individual tree size, pH-values in the topsoil and canopy openness, while there was no effect associated with tree diversity. Analysis of further biotic factors showed high mortality of *A. platanoides* in areas with a high cover of *Rubus* spp. in the herb layer, indicating species-specific susceptibility to different site conditions. Overall, low mortality (compared to other BEF experiments on arable land) suggests an advantage of establishing a BEF experiment within an existing forest matrix. Simultaneously, this study shows that differences in environmental context dependency among species need to be considered more explicitly, when recommending management strategies. To ensure successful establishment of reforestations with substitute tree species is the first step to efficiently counteract the massive loss of ash trees with the aim of maintaining biodiversity and ecosystem functioning.

1. Introduction

Effects of globalization have largely increased in recent decades and accelerated transport of species across biogeographic barriers all over the world (Seebens et al., 2017; van Kleunen et al., 2015). In their new ranges some of these introduced species negatively affect resident communities which can, in turn, impose severe consequences for local ecosystems, in particular, if they involve pathogens (i.e. trophic interactions) that bring about epidemic diseases (Mack et al., 2000; Rivers et al., 2022). One current example is the unintentional introduction of

the ascomycete *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya to Eastern Europe in the late 1990s (Kowalski, 2006). This pathogen causes the ash dieback disease which is now affecting European ash (*Fraxinus excelsior* L.) in its entire native distribution range with mortality reaching up to 69 % and 85 % in ash-rich woodlands and plantations, respectively (Coker et al., 2018). To date, there is a lot of research effort to control the disease and to identify “resistant genotypes” (Harper et al., 2016; Kirisits et al., 2016; Pliūra et al., 2017). However, forestry and silvicultural agents face the urgent challenge to deal with the extensive loss of such a key tree species and the subsequent

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transformation of formerly ash-rich forest stands (Broome et al., 2019). Ash dieback implies manifold consequences and affects ecosystem functioning at multiple levels. Most evidently, the progressing crown defoliation at the tree individual level and the loss of trunks (either due to subsequent mortality or as part of forest management actions anticipating the death that is imminent) can create large gaps in the forest canopy, thereby altering the light regime and consequently affecting understory composition (Turczański et al., 2020). Sites typically occupied by ash are characterized by high soil nutrient availability, where highly competitive understory species, such as *Rubus* spp., are likely to emerge after disturbance and prevent natural rejuvenation in these forest stands (Walter et al., 2016). Higher light incidence as well as increased competition create problematic challenges for forest managers trying to establish compensatory plantings in areas highly affected by ash dieback. At the same time, species directly associated with ash will likely decline or run the risk to go extinct (Hultberg et al., 2020; Mitchell et al., 2016b). Finally, forest ecosystems, which have been shaped by the unique functional configuration of the European ash, involving ecological traits such as rapidly decomposing litter and high bark pH, are prone to changes in their nutrient cycle, soil microbial and mycorrhiza fungi community (Mitchell et al., 2014).

From a forestry practitioner's perspective, the planting of alternative tree species is part of current recommendation strategies to mitigate substantial ecological impacts caused by ash dieback (Hill et al., 2019; Mitchell et al., 2016a). Accordingly, researchers have often aimed to identify functional matches and redundancies in ash and other tree species by comparing key characteristics, in order to use them as tree substitutes to alleviate otherwise expectable changes (Broome et al., 2019; Hill et al., 2019; Hultberg et al., 2020). However, decades of research especially in the field of Biodiversity-Ecosystem Functioning (BEF) have shown that impacts of species diversity are much more complex in forest ecosystems and can even be context- or scale-dependent (Ammer, 2019; Chisholm et al., 2013).

In recent decades, BEF research in forests has evolved rapidly: Starting from first identifying general relationships between tree species diversity and ecosystem functions and services in observational studies (Chisholm et al., 2013; Gamfeldt et al., 2013), approaches explicitly manipulating species diversity as a predictor in experimental studies are nowadays common for studying ecosystem responses also in complex and long-lived ecosystems such as forests (Bruehlheide et al., 2014; Scherer-Lorenzen et al., 2007; Verheyen et al., 2013). Most recent approaches even account for the increased complexity by studying multi-trophic relationships in these multi-layered ecosystems (Schuldt et al., 2018). However, the role of environmental context dependency has only scarcely been taken explicitly into account as most BEF studies with trees are working on a maximum of three to four sites (Bruehlheide et al., 2014; Scherer-Lorenzen et al., 2007; Verheyen et al., 2013). Some of them manipulate environmental conditions as an experimental subplot treatment along a tree diversity gradient (Germany et al., 2017; Trogisch et al., 2017). Yet, most of the tree biodiversity experiments worldwide (Paquette et al., 2018) are established and planted on open or cleared fields and are rarely conducted as enrichment planting into existing forests (Hector et al., 2011). The latter approach, however, is a more appropriate and realistic one for accompanying situations of forest transformation in the midst of global change involving ecological threats through calamities of pathogens, herbivores or climate-induced species losses. In fact, in experimental tree plantations, the local neighborhood and the degree as to which these neighbors might serve as hosts or non-hosts can have a crucial effect on the extent of fungal infection of trees. In temperate BEF-plantations, e.g., Hantsch et al. (2014) were able to show for *Tilia cordata* Mill. and *Quercus petraea* (Matt.) Liebl. that local tree diversity reduced fungal infestation by host-specialized fungal pathogen species. As a primary mechanism, positive impacts on ecosystem functioning by decreasing the level of fungal pathogen infestation can partly be ascribed to dilution of host species in the local neighborhood: for subtropical forests, Saadani et al. (2021) concluded

that diverse forests will suffer less from foliar fungal diseases. Indeed, foliar fungal infestation decreased with increasing tree species richness in subtropical (Rutten et al., 2021) and Mediterranean-type (Field et al., 2020) forest systems, whereas observational studies in temperate forest systems revealed a contrary pattern (Nguyen et al. 2016).

In the case of ash dieback, understanding the contextual impact of the disease on forest ecosystems plays a crucial role in developing strategies for forest regeneration and biodiversity conservation. While observations show that European ash trees are lethally attacked by the fungus independent of age class and site conditions (Pautasso et al., 2013), there is evidence that the extent of ash dieback and ultimately ash tree mortality may display environmental context dependency (Havrdová et al., 2017). European ash prefers fertile soils and (moderately) wet soil conditions although it also occurs on thermophilous sites (Walentowski et al., 2017). Several studies have suggested that wet soil conditions show higher probability of stronger fungal damage at the individual level (Erfmeier et al., 2019; Gross et al., 2014; Schumacher, 2011). For example, Turczański et al. (2020) recently analyzed the environmental factors affecting the disease in 27 Polish forest stands. The authors were able to link strong crown defoliation as an effect of ash dieback infection with a high soil pH and high contents of soil organic matter. Especially in the highly fragmented small forest patches of Northern Germany, ash is bound to small-scale transitional areas from wet alder-ash forests to fresh beech forests along small creeks or ditches. In this setting, natural conditions not only dictate environmental heterogeneity between forests but also within stands. Hence, the apparent shortfall of European ash and the need to test for functional alternatives (i.e., single tree species with similar fundamental niches or suitable tree species combinations) in habitats of existing forest ecosystems provide the unique opportunity to apply BEF research approaches to settings where practical reforestation is required. Since 2019, the project FraDiv studies effects of ash dieback and aims at mitigating the impacts of the fungal disease in existing forest ecosystems. The project within the Federal Programme for Biodiversity implies both an observational (FraDiv^{obs}) and an experimental (FraDiv^{exp}) platform in temperate forests located in the northernmost part of Germany. FraDiv^{exp} applies BEF approaches, thus offering a suitable platform for studying Biodiversity-Ecosystem Functioning relationships over a wide environmental range within forest stands in transformation. Similar to the Sabah experiment situated in tropical forests of Borneo (Hector et al., 2011), FraDiv^{exp} was established in the existing matrix of thinning tree layers and opening forest canopy. Five tree species characteristic of temperate forest ecosystems, including European ash, are analyzed across a soil moisture gradient over multiple sites addressing a possible context dependency of ash mortality caused by *H. fraxineus*, while taking explicitly BEF relationships experimentally into account. To our knowledge, this is the first time to make use of a forest dieback event as a base to establish a BEF experiment directly underneath the remains of collapsing canopies of temperate forests and thus to combine the need for reforestation and addressing context dependency in BEF research. This way, this project's overall aim is to give recommendations for species conservation in the wake of ash dieback based on knowledge from experimental reforestations.

In this study, we will present first insights into the initial phase of tree establishment in FraDiv^{exp}. Specifically, we will a) analyze the environmental variation between sites and b) test for effects of experimental tree diversity, tree species identity (i.e., the effect of having a particular species present in the exact mixtures planted per plot) and co-varying environmental factors between sites on mortality of saplings.

2. Methods

2.1. Study sites

The FraDiv^{exp} research platform was established in the eastern region of Schleswig-Holstein, Germany, in winter 2019/2020. With a

mean annual temperature of 8.9 °C (1998–2010) and a mean annual precipitation of 823 mm (1981–2010) all sites can be assigned to sub-oceanic climate conditions (DWD, 2017). All experimental sites are located on recent moraines formed during the last (Weichselian) glaciation. In this characteristic moraine landscape, Luvisols are the prevailing soil types. At sites with high soil moisture, moderate textural differences often lead to the formation of Stagnosols. At groundwater-affected sites, Gleysols are found (Table S.1). On these soils, ash is varying in proportions from moist base-rich sites dominated by beech (*Fagus sylvatica* L.) to wet forest sites mixed with black alder (*Alnus glutinosa* (L.) Gaertn.) and dominating the moderately wet forest sites in a mixture with other deciduous trees like European hornbeam (*Carpinus betulus* L.) (Härdtle, 1995). Today, the forests of this landscape are largely fragmented involving small patches of ancient forest remnants and with a majority of reforested stands. With only 11 % (173,412 ha) of the total area covered by forest, Schleswig-Holstein is the federal state with the lowest proportion of forested area in Germany (BMEL, 2016).

In total, the experiment comprises 12 ash-rich or formerly ash-rich sites established in forest fragments differing in size. Six sites are located in separate small forest patches in the northeastern part of Schleswig-Holstein whereas six further sites belong to one larger forest complex in the southeastern part of Schleswig-Holstein (Fig. 1). For each of these two sets of sites, we aimed at covering the majority of the ecological range along which *F. excelsior* is growing in Schleswig-Holstein, including each two sites affected by groundwater and four sites influenced by stagnating water or representing Luvisols. Study site selection was restricted to mineral soils only and additionally excluded

on purpose the driest sites and the wettest, peatland sites which are dominated by *F. sylvatica* and by *A. glutinosa*, respectively. The final shape and size of the individual experimental sites was determined by natural forest heterogeneity and had to take into account internal structural conditions due to ditches and trails. Overall, sizes of sites range between 0.7 and 2 ha. All sites correspond to ancient forests with long development continuity (Härdtle et al., 2008), with a near-to-natural management for at least 20 years prior to the establishment of the experiment, and are privately owned by various persons (for further details see Table S.2).

2.2. Selection of tree species for the experiment

For the selection of alternative tree species only deciduous tree species were taken into consideration, which are a) native to Northern German lowlands, b) adapted to site conditions on which ash is usually found and c) capable to build a dominant tree cover in the terminal phase of deciduous forest succession. In addition, regionally adapted planting material had to be available for the experiment. From this preselection two mainly arbuscular mycorrhizal (AM) and two mainly ectomycorrhizal (ECM) tree species were chosen in consultation with local forest practitioners. Beside *Fraxinus excelsior* L. (AM), the final selection includes *Acer platanoides* L. (AM) (Norway maple), *Ulmus laevis* Pall. (AM) (European white elm), *Carpinus betulus* L. (ECM) (European hornbeam) and *Tilia cordata* Mill. (ECM) (Small-leaved lime) (Brundrett and Tedersoo, 2020; Harley and Harley, 1987; Lang et al., 2011). Some of these species are also considered for compensatory plantings in

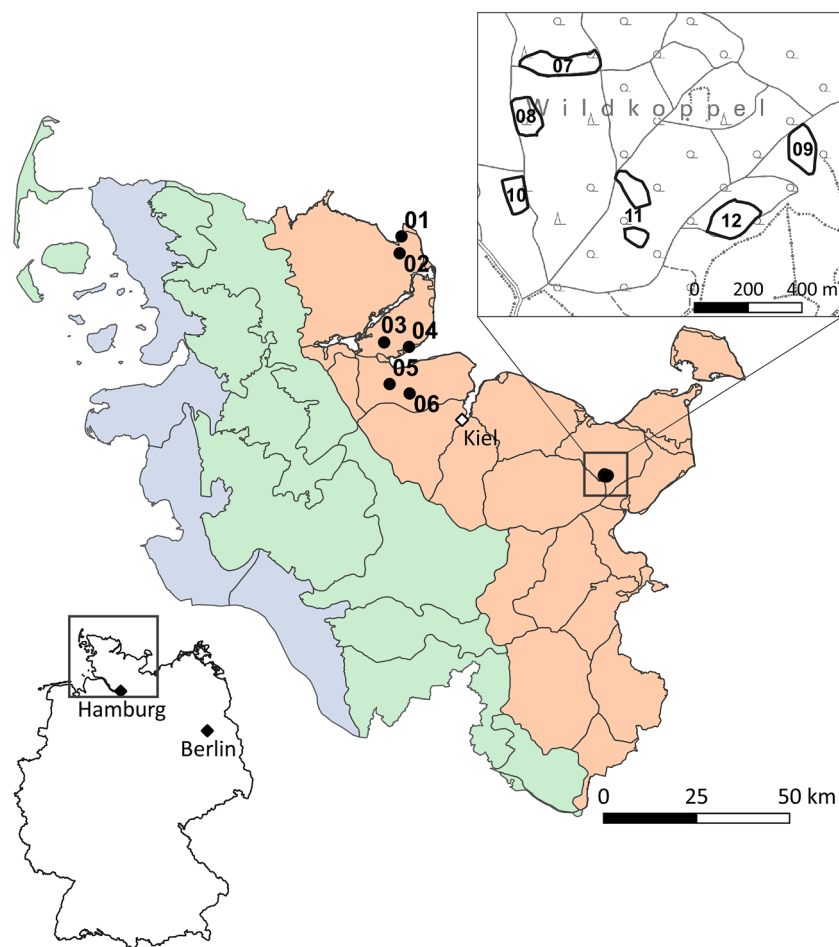


Fig. 1. Location of all experimental sites. Map of the three major landscape types of Schleswig-Holstein (blue = marshland, green = ancient moraines, red = recent moraines) indicating the location of the 12 experimental sites. The small map at the top right details the exact location of the southern experimental sites 7 – 12 in one large forest complex. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reaction to ash dieback in different Northern European countries (Hill et al., 2019; Hultberg et al., 2020; Mitchell et al., 2016a).

2.3. Experimental design – Sites and plots

In the experiment, a richness level gradient of 0 (control), 1, 2, 4 and 5 tree species was realized on each site. Given the experimental dimensions with regard to tree species richness and site availability in number and size, we were able to realize all possible combinations of the five tree species for each richness level. This results in 5, 10, 5 and 1 different mixtures for the richness levels 1, 2, 4 and 5 species, respectively, adding up to 21 distinct mixtures to be established on each site (Fig. 2). In contrast to other BEF designs, where one has to constrain to a subset of the pool of available combinations via random selection or the explicit application of a broken-stick design (Bruehlheide et al., 2014), we thus adhered to the realization of a full design. This procedure conforms to the intention that – different from the general interest in the effect of biodiversity, forest practitioners, in the end, are specifically interested in species identity effects of particular tree combinations.

Each of the described mixtures was realized in a north-oriented 10×10 m plot with a minimum distance of 4 m between plots. On each of the 12 sites, one additional plot was installed with no planting as a control, thereby adding up to a complete set of 22 plots per site and amounting to a total of 264 plots for the entire experiment. While the original arrangement of plots envisaged a regular distribution according to a grid, structural heterogeneity within the forest stands required individual plot-wise adjustment along the cardinal points for the establishment, thus within-site location of plots was largely determined by natural conditions of the forest stands, such as the presence of trees, ditches and small-scale changes in (micro-) site conditions. Final plot areas had to be as homogeneous as possible, keeping the number of mature trees, stumps and rocks to a minimum and thus to reduce the necessity of severe intervention and disturbance due to additional silvicultural measures and preparation. All forest stands display some

naturally given heterogeneity and are differently subjected to ash tree losses resulting in situations of high light exposure and/or a moderate to high cover of bramble bush (*Rubus* spp.) or other nitrophilous species such as *Urtica dioica* L. or various competitive grass species. Experimental treatments (i.e., species richness levels and species combinations) were randomly assigned to plots within-site. However, in order to avoid overrepresentation of richness levels in these particular environmental settings by chance, the assignment of treatments was verified in a two-step procedure: In a first step, for each site multiple sets of plot assignments were randomly generated for each of the twelve sites. Each set was then inspected for a within-site overrepresentation of richness levels in areas of advanced degradation. For this purpose, a cover greater than 60 % of either *Rubus* spp. or the total herb layer was defined as a sign of advanced degradation due to naturally occurring clearing. In a second step, the first three sets of proper assignments in this regard were then inspected for overrepresentation across all sites (i.e. to make sure, for example, that particular species mixtures or monocultures do not come along with high light exposure or accumulate at edge positions by the majority across sites).

Within plots, trees were arranged in a regular grid of each ten individuals with a distance of 1 m per row and column corresponding to a planting density of 1 tree per m^2 (100 trees per $100 m^2$, see discussion on planting density in Bruehlheide et al. 2014). Tree species identities were randomly assigned to the planting positions. In mixtures, different species were consistently planted in the same proportion (i.e., 50 individuals per species in 2-species mixtures, 25 individuals per species in 4-species mixtures and 20 individuals per species in the 5-species mixture). Future research will focus on the central 6×6 trees as the core area of the plots (in accordance with Bruehlheide et al. 2014) to overcome the influence of plot edge effects. To avoid underrepresentation of tree species identities in the plot core area we discarded assignments where more than 1/3 of the individuals of one or more species were found in the plot margin.

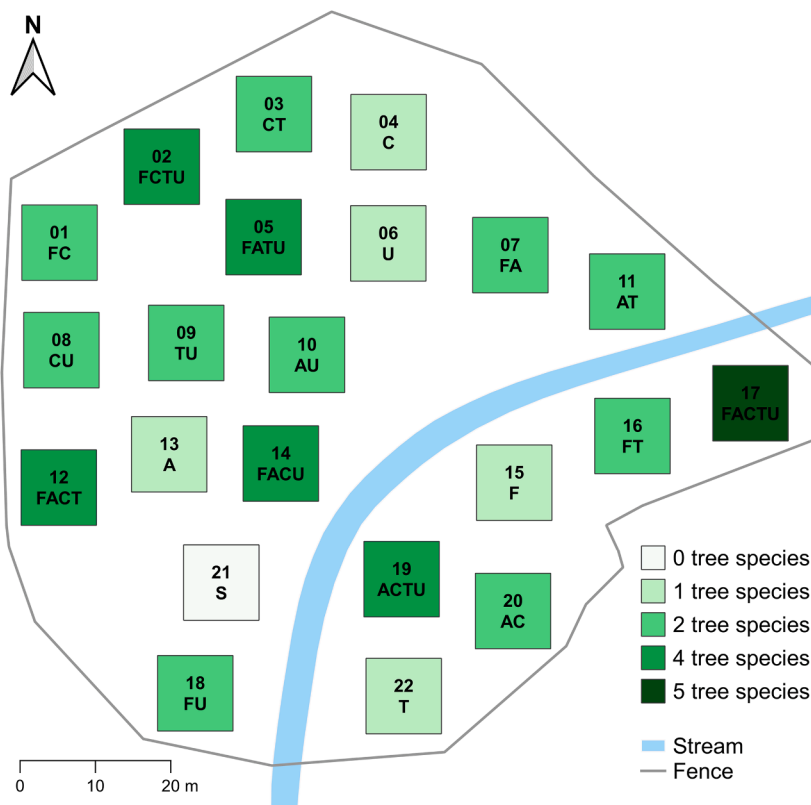


Fig. 2. Schematic illustration of plots located in one of the experimental forest sites. Depicted are the 22 experimental plots and major forest structures influencing the location of plots within this site. Plots are numbered 1 – 22 to which unique species combinations, as depicted by the letters below the plot numbers, were randomly assigned. Letters abbreviate tree species planted in the plots (F = *Fraxinus excelsior*, A = *Acer platanoides*, C = *Carpinus betulus*, T = *Tilia cordata*, U = *Ulmus laevis*) while the control plot where no trees were planted is marked with S (succession). The color gradient indicates the number of tree species included in the mixture.

2.4. Site preparation and planting procedure

Site maintenance and clearing was provided by the forest managers involved in this project. For safety reasons dead or severely damaged trees were removed from all sites prior to planting in early summer 2019. In addition, stands were moderately thinned to achieve a corridor of comparable light conditions aiming at a canopy openness corridor between 30 and 60 % on all sites. To exclude effects of browsing all sites were fenced before planting. For all plots, a baseline monitoring of the herb layer vegetation was conducted in July 2019 prior to planting. Afterwards plot areas were cleared from all remaining trees and shrubs. Prior to planting, the herb layer vegetation had been mowed in autumn 2019. No heavy machinery was used in order to avoid soil compaction.

Planting material for all five tree species was purchased at two local tree nurseries as bare rooted two-year old tree saplings of Northern German provenances. Planting took place in three steps: 1) marking of planting positions on the ground, 2) assignment of individuals by species to their positions according to the prepared planting sheets and 3) manual planting of bare root saplings (spade planting). The planting campaign comprised 25,200 sapling individuals and was carried out in December 2019 and January 2020. Each sapling was labelled with its unique plant ID. To ensure initial establishment of the saplings weeding was repeated for each plot from August to September 2020. The herb layer was cut back motor-manually to approximately 30 cm above ground irrespective of the initial vegetation height. This includes removal of natural recruitment of tree juveniles that come up with natural dispersal events from neighboring reproducing trees. Dead saplings were replanted once in November 2020.

2.5. Data collection

For each sapling, plant height (measured as absolute shoot length) and basal diameter were measured shortly after planting in February and March 2020 and will serve as baseline data for future analysis. In the subsequent weeks, a fungal infection on *A. platanoides* individuals was observed. In July 2020, shoot damage such as effects from the fungal infection or mechanical damage from planting were recorded in seven classes from 0 (no damage) to 1 (complete shoot damaged): 0, 0.01 – 0.1, 0.11 – 0.25, 0.26 – 0.5, 0.51 – 0.75, 0.76 – 0.9, 0.91 – 1. After one growing season, in November 2020, a survival survey of all saplings was conducted.

To account for abiotic covariation affecting initial establishment success and survival, soil samples were taken in February 2020 in all plots to determine pH, total carbon (C) and total nitrogen (N) contents. In each plot, four samples (one from each of the four plot quadrants) were taken from the mineral top soil layer and merged before drying and analysis. Soil pH was determined with a single rod glass electrode in a 1 N KCl solution. Total C and N contents of the soil were analyzed with a gas-phase chromatograph following the Dumas method (Saint-Denis and Goupy, 2004). For all plots, soil types were recorded along drill stick profiles to a maximum depth of 1 m in September 2021. Field capacity was derived from mean values for each soil type with an estimated medium bulk density and finally added up for each plot (AG Boden, 2005). At the end of August 2020, hemispherical photos were taken with a Lumix DMX-GX80 camera and a Lumix G fisheye lens at a fixed height of 1 m above the ground in the center of each plot to assess light conditions. Photos were processed in MatLab (R2021a) and analyzed with WinSCANOPY (2021a) to obtain values for canopy openness, which is defined as the fraction of open sky in the hemisphere above the camera lens.

Biotic variables examined refer to herb layer composition. Two vegetation surveys were conducted in the first year after planting, including the record of early spring geophytes in April 2020, and a full vegetation survey in June and July 2020. Plant species cover was assessed by using the Londo scale (Londo, 1976), whereas total vegetation cover was recorded as percent coverage separately by each

vegetation layer: herb layer (herbaceous and woody species ≤ 1 m height), shrub layer (woody species 1 – 5 m height), tree layer 2 (subordinate trees greater than 5 m height), tree layer 1 (dominant trees greater than 5 m height). In the *Rubus* genus, *R. caesius* and *R. idaeus* were identified on the species level whereas *R. fruticosus* agg. was identified to species group level without further differentiation into species or subspecies. Total cover of the herb layer (in %) and cover of *Rubus* spp. used as covariates in mortality analysis (see below) were derived from the summer survey.

The initial infestation state of ash dieback of the remaining mature ash trees at each site was considered a crucial predictor for future development of planted ash saplings. While most of the variables refer to the plot level, additional information as to previous ash infestation characteristics of mature trees are only available at the site level. The magnitude of damage caused by *H. fraxineus* was assessed by determining crown damage and basal necrosis for all mature ash trees with a diameter at breast height (DBH, diameter at 1.3 m height) of at least 15 cm. Crown damage was estimated as the amount of defoliation in the ash crown in percent. Basal necrosis was determined by measuring root collar circumference and horizontal necrosis extension 10 cm above ground and calculating the proportion of necrotic tissue. Finally, mean values of crown defoliation and basal necrosis were calculated for each site.

2.6. Data analysis

Environmental variation between and within sites was analyzed with a principal component analysis (PCA) on the plot level. In this analysis, we included pH, C:N ratio, field capacity [mm] and canopy openness [%] to characterize abiotic site conditions. As biotic variables, cover of *Rubus* spp. as well as total herb layer cover was included as proxies for disturbance and increased productivity, respectively. To check for differences with regard to the infestation situation between sites, mean crown defoliation of all mature ash trees per site were calculated and included in the PCA. All variables were scaled and centered prior to analysis.

In subsequent analyses, mortality served as response variable. Mortality of planted saplings after one full growing season was analyzed with a generalized linear mixed effects model (GLMM) using a model selection process. The full model included species identity as a fixed factor, tree species richness as continuous predictor, initial sapling height, pH, C:N ratio, field capacity, canopy openness, herb layer cover and cover of *Rubus* spp. as continuous covariates, and all two-way interactions of the covariates with species identity to account for species-specific effects of the environmental context. All predictors were non-correlated with variance inflation factors (VIFs) < 3 (Zuur et al., 2010). To account for spatial correlations, plot ID nested in site ID was set as a random effect. The model was fitted with glmmTMB (Brooks et al., 2017) using a cloglog-link function and binomial error distribution. Model selection was run with MuMIn:pdredge (Barton, 2020), keeping species identity fixed in all models. Best models were determined by lowest AICc and models with delta AICc of < 2 were assumed to be equally explanatory. However, since inference did not differ between best models, only results of the most extensive of these models are given. The DHARMA package (Hartig, 2022) was used for model diagnostics. Car:Anova (Fox and Weisberg, 2019) and emmeans (Lenth, 2022) were used for post-hoc testing and further model interpretation. Variance components were extracted using the R-packages insight (Lüdtke, 2022a) and parameters (Lüdtke, 2022b).

All data analysis were performed in R (Version 4.0.5) (R Core Team, 2021).

3. Results

3.1. Site and plot characteristics

Abiotic site conditions varied strongly among and within sites (Table 1, S.3). pH values ranged from 2.7 to 6.5 and C:N ratios spanned from 9.9 to 21.2 with median values of 4.0 and 12.8, respectively. Values of field capacity varied between 131.1 mm up to 195.9 mm, while canopy openness reached a maximum of 51.3 % across all plots with a median of 14.3 %. Herb layer cover comprised the full range from nearly absent vegetation (1 %) to entirely covered (100 %). In total, 137 distinct species and further 19 plants, which could only be identified on the genus level, were recorded. Total *Rubus* spp. cover ranged between 0 and 95 % (Londo: 0 – 9) with a median of 40 %.

PCA divided plots within sites based on the habitat characteristics along four axes and summarized site differences. All four axes combined explained 79.4 % of the total variation. The first and the second axes explained 29.3 % and 18.9 %, respectively, whereas the third and the fourth axes still explained additional 16.9 % and 14.3 % respectively (Table 2). The first principal component (PC1) describes total herb layer cover (Pearson correlation $r = 0.73$, $P < 0.001$) and pH (Pearson correlation $r = 0.77$, $P < 0.001$) in the positive direction. C:N ratio (Pearson correlation $r = 0.58$, $P < 0.001$) significantly correlates positively with the second principal component while ash crown defoliation significantly correlates with both the second and the third principal component (Pearson correlation PC2: $r = 0.61$, PC3: $r = 0.54$, for both $P < 0.001$) positively. Simultaneously, the third principal component significantly correlates negatively with *Rubus* spp. cover (Pearson correlation $r = -0.74$, $P < 0.001$). The fourth principal component is strongly correlated with field moisture capacity (Pearson correlation $r = 0.90$, $P < 0.001$).

In the dimensional space formed by PC1 and PC2, most sites are intermixed and only very few sites, such as site 3, can be associated with similar site conditions at the plot level, as expressed in a close cluster (Fig. 3). Highest within-site variation was found in site 10 with plots scattering widely along the second and the first PCA axis, thus varying greatly in multiple abiotic and biotic site conditions. For most sites, however, the variation of biotic and abiotic conditions of the plots with regard to the variables studied here seems to comprise a similar range.

3.2. Sapling mortality

Generalized linear mixed effects model showed a mean mortality of 5 % over all planted saplings, after one full growing season (Fig. 4). With 17.4 %, mortality was highest in *A. platanoides*. For *F. excelsior* and *T. cordata*, mortality was 2.8 % and 2.7 % of the saplings, respectively. Lowest mortality was recorded in *U. laevis* and *C. betulus* with only 1.1 % and 0.8 %, respectively.

74 % of saplings showed no damage along the main shoot. In *A. platanoides* 20 % of all planted saplings showed more than one quarter of the main shoot damaged while for each of the other species it was < 3 % (Fig. S.1).

Results of the GLMM show that mortality of the saplings differed

significantly among species. However, across all species, mortality was significantly reduced with increasing initial sapling height and increasing soil pH, whereas mortality increased with increasing openness of the canopy (Table 3 & S.4, Fig. 4). The GLMM for mortality has a marginal R^2 (providing the variance explained by fixed effects only) of 0.505, while the conditional R^2 (considering both fixed and random effects) is 0.668 (Table 3). Variance of the random factors mainly resulted from plots nested in sites (0.70) rather than only from sites (0.12).

There was no significant effect of tree species richness on sapling mortality. Yet, there was a marginal trend ($P = 0.07$) suggesting that mortality tended to be larger on plots with higher species richness levels. Initial sapling height displayed a significant effect suggesting higher mortality for saplings smaller in size than for the larger ones (Fig. 5 b.1/2). Significant interaction of sapling height with species identity indicates that *F. excelsior* responded differently compared to all other species (Table S.4, Fig. 5 b.1/2).

The model also shows abiotic variables affecting mortality differently. Mortality probabilities of all tree species significantly increased with increasing canopy openness (Fig. 5 a.1/2). Among edaphic variables, pH was the only significant predictor for sapling mortality, which was displayed by the significant interaction between pH and species identity: in contrast to ash, *A. platanoides*, *T. cordata* and *C. betulus* displayed an increase in mortality with increasing pH in the upper mineral soil layer (Fig. 5 c.1/2).

Among biotic site factors, both total cover of herb layer and cover of *Rubus* spp. showed significant interaction effects with species identity, displaying opposing effects on sapling mortality for three species. Mortality of *A. platanoides* decreased with increasing herb layer cover, while *T. cordata* and *U. laevis* tended to show higher mortality with increasing herb layer. In contrast, with increasing *Rubus* spp. cover, the directions of responses were reversed with increasing mortality at high *Rubus* spp. cover for *A. platanoides* and decreasing responses for *T. cordata* and *U. laevis* (Fig. 5 d.1-e.2).

4. Discussion

4.1. Site heterogeneity

There is broad evidence that forests with their highly structural nature and multiple layers also encompass a broad range of environmental variation (Dahlgren and Ehrlén, 2009; Forrest Meekins and McCarthy, 2001; Laliberté et al., 2009) including differences between sites and plots and even tree-related microhabitats (Asbeck et al., 2021; Winter and Möller, 2008). Characterization of the FraDiv^{exp} sites and plots reveals the complexity of forest ecosystems and the multitude of factors and interactions that must be considered. In the present dataset, stand characteristics vary more at the plot scale than at the site scale as evidenced by the high proportion of random variation due to plots nested in site (70 %) in the generalized linear mixed effects model. This differs, for example, from cork oak forests, where Quilchano et al. (2008) found a general trend of increasing heterogeneity with growing spatial scale and where only few environmental parameters showed greater within-forest site than between-forest site variation. Despite clear rules for study site selection to maximize comparability of ash stands, the high overall variation in our dataset confirms that, in Northern German forests, ash is usually located in small-scale transitions of different habitats rather than covering extensive homogeneous environmental conditions. This variation needs to be considered explicitly when planning experimental settings and plantations. Bruelheide et al. (2014) recommend a full characterization of the co-varying environmental conditions (“ecosphere”) when establishing a tree BEF experiment, in order to be able to account for environmental heterogeneity during statistical analysis when exploring biodiversity effects. At the same time, heterogeneity, especially in regard to soil moisture, was shown to be one of the main effects explaining variations in the infestation situation of ash trees

Table 1

Biotic and abiotic environmental characteristics of the 264 investigated plots (minimum, median, mean and maximum values among all plots).

	Min	Median	Mean	Max
pH	2.7	4.0	4.2	6.5
C:N	9.9	12.8	13.1	21.2
Field capacity [mm]	131.1	165.1	163.9	195.9
Canopy openness [%]	3.1	14.3	15.7	51.3
Ash defoliation [%]	13.7	43.0	42.9	64.8
Herb layer cover [%]	1	80.0	69.8	100.0
<i>Rubus</i> spp. cover [Londo]	0	0.4	1.4	9

Table 2
Eigenvalues, cumulative explained variance, Pearson correlation coefficient (r) and p-values of the principal component analysis for all biotic and abiotic parameters in relation to the first four PCA axes. Significant p-values are given in bold (significance levels: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1).

	PC1		PC2		PC3		PC4	
Eigenvalues	2.049		1.324		1.180		1.004	
Cumulative explained variance [%]	29.275		48.193		65.054		79.394	
	r	p-value	r	p-value	r	p-value	r	p-value
pH	0.768	< 0.001	−0.257	< 0.001	0.190	0.002	−0.006	0.922
C:N	−0.590	< 0.001	0.578	< 0.001	−0.109	0.077	−0.020	0.749
Field capacity [mm]	−0.007	0.909	0.350	< 0.001	0.105	0.089	0.903	< 0.001
Canopy openness [%]	0.696	< 0.001	0.451	< 0.001	0.186	0.002	0.017	0.787
Ash defoliation [%]	0.259	< 0.001	0.613	0.890	0.545	< 0.001	−0.341	0.014
Herb layer cover [%]	0.731	0.01	−0.009	< 0.001	−0.496	< 0.001	0.152	< 0.001
Rubus spp. cover [%]	0.159	< 0.001	0.471	< 0.001	−0.737	< 0.001	−0.220	< 0.001

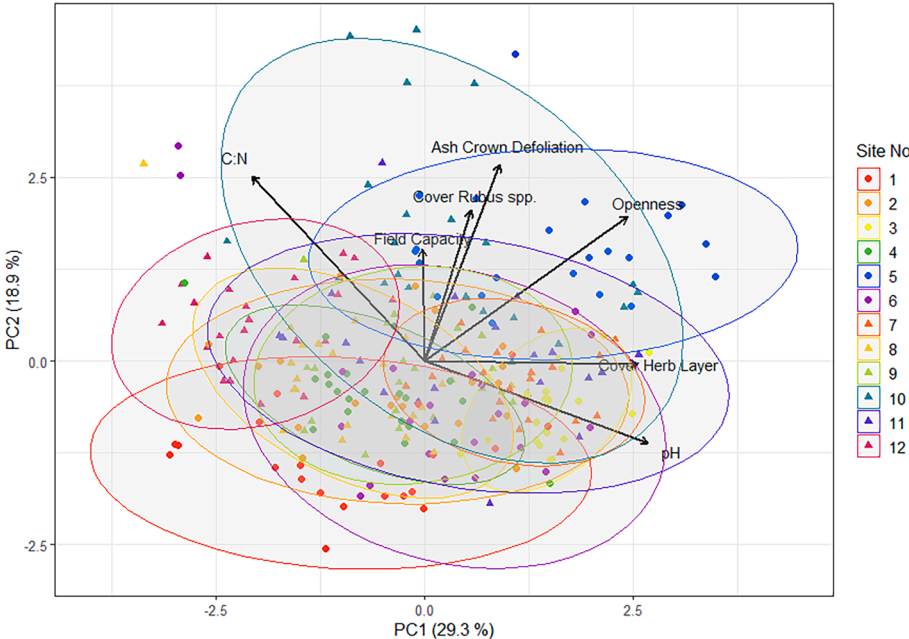


Fig. 3. Biplot of the PCA showing plot distribution along environmental gradients. PCA biplot of principal components 1 and 2, including plots grouped by area (circles = sites 1 – 6 situated in the northeastern part of Schleswig-Holstein, triangles = sites 7 – 12 situated in the southeastern part, see Fig. 1) and experimental site (color gradient) and variables as vectors. All parameters used in analysis are shown as arrows. Soil chemical parameters (pH, C: N), field capacity [mm], canopy openness (Openness [%]) and biotic parameters (total cover of the herb layer [%], cover of *Rubus* spp. [%]) were included as per-plot values, whereas ash crown defoliation [%] of the remaining mature ash trees was included as mean per site. For names and information on site numbers, see Table S.2.

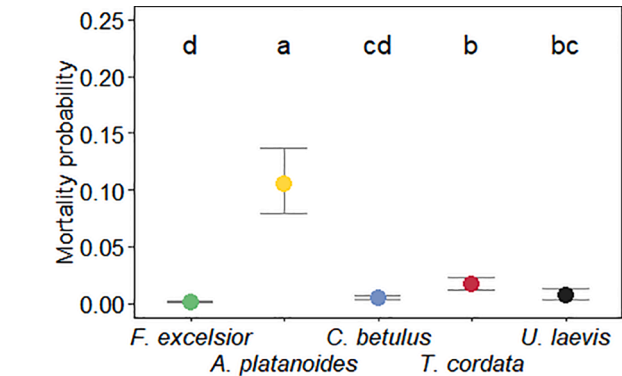


Fig. 4. Predicted tree mortality probability per species. Depicted are predicted results from the optimal generalized linear mixed effects model. Mean mortality probabilities for each tree species. Whiskers show 95 %-confidence intervals. Different letters indicate significant differences according to post-hoc test.

(Chumanová et al., 2019). Moreover, soil drivers, among those C:N ratio, CaCO₃ and groundwater table, were shown to affect the ash regeneration infestation rate (Turczański et al., 2022). This underlines the need for taking context dependency into account not only when

Table 3
Type III ANOVA statistics on the optimal generalized linear mixed effects model predicting mortality of the planted saplings. Significant effects are given in bold (significance levels: *** < 0.001; ** < 0.01; * < 0.05; . < 0.1).

	Chisq	Df	Pr (>Chisq)	
(Intercept)	7.947	1	0.901	
Species	46.591	4	< 0.001	***
Plant height	79.139	1	< 0.001	***
Richness level	3.277	1	0.070	
pH	15.577	1	< 0.001	***
C:N ratio	2.131	1	0.144	
Openness	3.983	1	0.046	*
Cover herb layer	1.879	1	0.170	
Cover <i>Rubus</i> spp.	0.060	1	0.806	
Plant height: Species	49.477	4	< 0.001	***
Richness level: Species	1.543	4	0.819	
pH: Species	101.394	4	< 0.001	***
Herb layer: Species	33.546	4	< 0.001	***
<i>Rubus</i> spp.: Species	60.801	4	< 0.001	***
% Variance explained by				
Fixed effects			50.5	
Random effects			16.3	
Residuals			33.2	

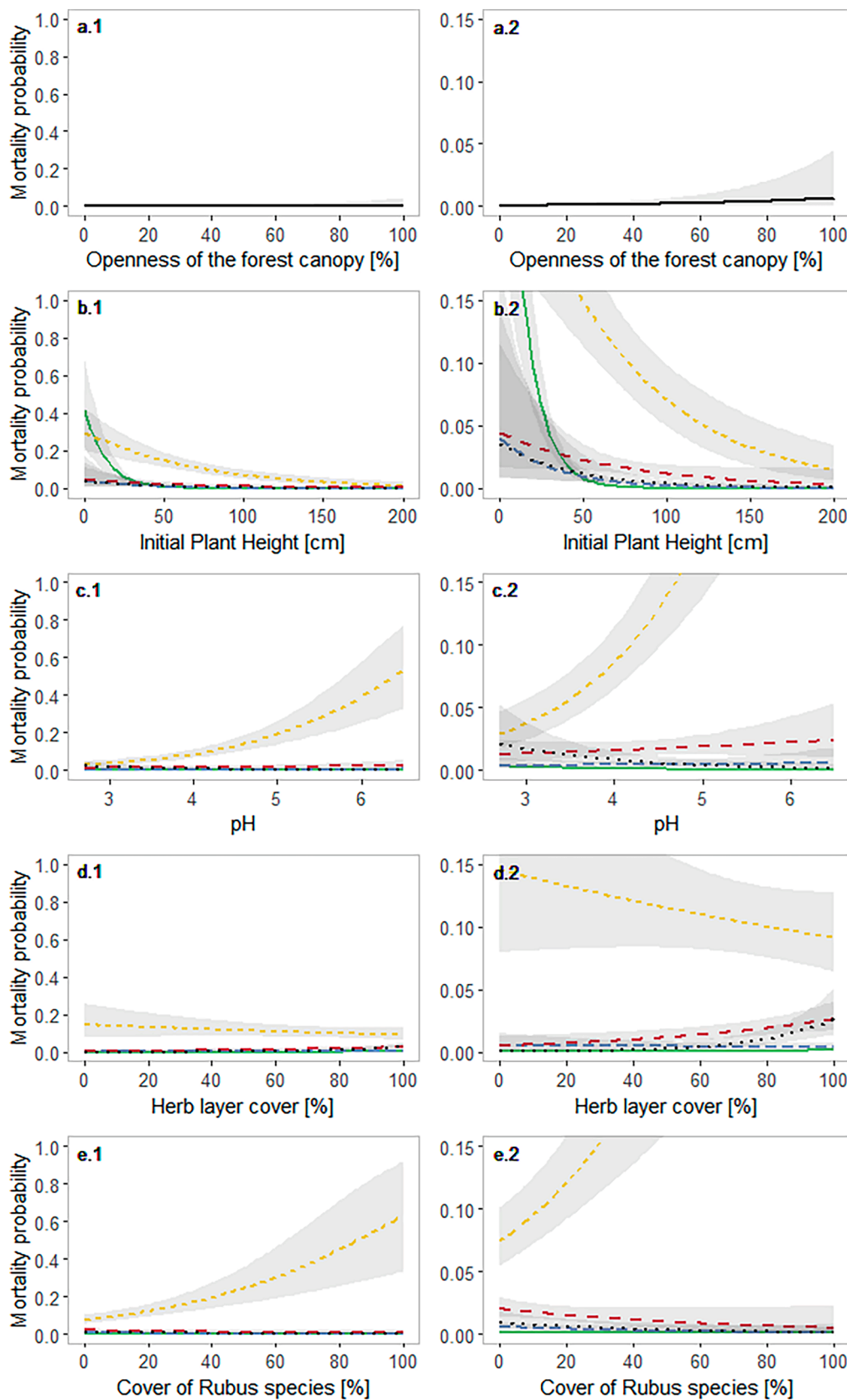


Fig. 5. Predicted tree mortalities for significant covariates. Predicted mortality probabilities from the optimal generalized linear mixed effects model of the significant variables canopy openness (a.1, a.2), initial sapling height (b.1, b.2), pH (c.1, c.2), herb layer cover (d.1, d.2) and *Rubus* spp. cover (e.1, e.2). For canopy openness only the main effect is given, for all other variables species-specific effects are shown (green = *F. excelsior*, yellow = *A. platanoides*, blue = *C. betulus*, red = *T. cordata*, black = *U. laevis*). Please note: panel 2 always enlarges the lower y-axis-section to improve visualization. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

situating experimental setups in forest ecosystems but also when developing guidelines for forest practitioners in the current phase of forest transition in (formerly) ash-rich forest ecosystems.

4.2. Sapling survival

With a total mortality of < 5 % across all sites, the initial establishment of the experimental platform FraDiv^{exp} was successful. Establishment rates of more than 95 % represent values far higher than achieved in similar afforestation projects in temperate regions (Don et al., 2007; van de Peer et al., 2016). For the BIOTREE experiment in Germany, for example, mortality rates for these species at two different sites were mostly below 20 % (Don et al., 2007; Scherer-Lorenzen et al., 2007) but still far higher than at the FraDiv^{exp} sites, which the authors ascribed to an extremely dry and warm summer in the year of planting in that region. Besides other factors influencing sapling survival (i.e. quality of the planting material) and independent of particular seasonal effects, this effect might be a positive by-product of enrichment planting into forests that provide more convenient and more balanced microclimatic conditions thereby favoring the establishment of juvenile trees (De Frenne et al., 2021).

After one vegetation period, tree species diversity showed no significant effect on sapling mortality, yet, a slight positive trend. This is in line with reports from multiple forest BEF experiments, which concluded that tree mortality is not connected with tree species diversity even multiple years after establishment (Healy et al., 2008; Liang et al., 2007). Grossman et al. (2018) provide a summary of literature assessing survival as one component of tree performance in forest BEF experiments (as framed in the TreeDivNet). In most of these studies, mortality was not affected by the respective tree diversity gradient applied. For temperate tree species, van de Peer et al. (2016) reported that survival was affected by tree diversity if considered separately for single tree species. However, these effects differed in direction as well as in magnitude, and there was no general overall diversity effect on sapling survival. Even though our analysis showed an overall marginal trend in increasing sapling mortality with higher species diversity this trend disappeared in interaction with species identity. Thus, we cannot confirm at this time of the experiment that there are benefitting species-specific effects of tree diversity in regard to mortality. However, the overall diversity trend found in FraDiv^{exp}, although not significant, indicated increased mortality at high levels of species diversity rather than biodiversity insurance. This could be in accordance with a selection effect of diversity on mortality, suggesting that more diverse plots are more likely to contain a high share of species that tend to die more easily (Grossman et al., 2018; Loreau and Hector, 2001). Yang et al. (2013) found a similar pattern for plantations of the subtropical BEF-China experiment and argue that this is most likely due to the more challenging planting procedure in high diversity mixtures. Higher methodological challenges in handling several species appropriately at high diversity plots might also contribute to a higher mortality in these plots in our experimental setting. Since, in BEF-China, this effect could not be validated in the years after replanting of dead trees, it was very likely caused by handling issues rather than BEF relationships (Huang et al., 2018; Yang et al., 2013). While diversity, here, did not yet affect tree mortality, we expect selection and complementarity as components of diversity effects to act on tree performance (such as growth, biomass and functional traits) just as it was shown for tropical (Healy et al., 2008; Potvin and Gotelli, 2008) and subtropical (Huang et al., 2018) forest BEF projects. Mechanisms of positive diversity effects may involve resource partitioning, facilitation, pathogen dilution and biotic interactions (Trogisch et al., 2021) and are particularly expected to increase with time (Bongers et al., 2021; Cardinale et al., 2007).

In accordance with previous reports we found species identity rather than species diversity to be one of the main drivers of mortality (Don, 2007; Potvin and Gotelli, 2008; van de Peer et al., 2016). As there is some evidence of fast disease progress in young ash trees (Enderle et al.,

2017), we expected *F. excelsior* to show the highest mortality rates among all of the five tree species. Surprisingly, ash mortality did not exceed 3 %, which amounts to only 143 individuals, after the first vegetation period and thus, also involving a first possible infection cycle with *H. fraxineus*. This could be partly explained by disturbance of the litter layer during plot preparation and planting and thus reduction of the infectious material, which in turn would lead to a reduced infection pressure during the following year. However, in Norwegian forest stands, Timmermann et al. (2017) also recorded only few dead individuals one year after starting to monitor healthy juvenile ash trees. Yet, mortality increased rapidly in the following years, so that again, the current state is just a snapshot of the momentary state. Thus, even for young and small ash individuals, ash dieback might require multiple years of infection to become lethal.

For *A. platanoides*, Don et al. (2007) reported first year mortality rates of 8 % and 12 % on two sites of the German BIOTREE experiment, respectively, which remained low on one site but rose up to 37 % on the second site in the following years. In comparison, Kerr and Niles (1998) documented survival rates as high as 88 % eight years after planting on the British Isles. In the present study, mean mortality of Norway maple across all FraDiv^{exp} sites was 17.4 % and thus significantly higher than the other four tree species planted. The cause was most likely infection with a generalist fungal species observed only on *A. platanoides* saplings and identified as *Botrytis cinerea* Pers. (grey mold). The fungus, probably originating from the nursery, attacked the terminal shoot and resulted in an increased number of severely damaged Norway maple specimens. We cannot confirm this infection to be the primary agent for maple tree mortality but we assume that it at least weakened saplings and potentially amplified negative effects of environmental factors on survival of saplings. Mortality rates for *T. cordata* ranged between 0 % and 4.8 % between sites with a mean mortality of 2.7 % (Table S.5). For the other two tree species, *C. betulus* and *U. laevis*, recorded mortality was < 1.5 %. The low number of dead individuals (e.g., 57 out of 5,040 individuals in *U. laevis*) limits the interpretation of species-specific interactions but, in contrast, highlights that *U. laevis* and *C. betulus* are suitable alternative tree species in ash rich forest ecosystems in regard to establishment success.

4.3. The meaning of covariation – Indicators for survival

Overall high significance values were due to co-varying effects of species performance and site for the failure of successful tree individual establishment. First-year sapling mortality was affected not only by species identity, but also by initial size and environmental parameters. This is in accordance with reports from Shen et al. (2020), who found initial size of trees to be more important than neighborhood effects. In the present study, e.g., very small sapling individuals tended to die more often and this effect differed between species. While mortality for *T. cordata*, *U. laevis* and *C. betulus* increased only slightly for saplings below ~ 30 cm, mortality increased rapidly in small *F. excelsior* individuals. In the nutrient-rich and rather wet (formerly) ash-rich forest sites, environmental stresses such as drought are minimized. Under these conditions, larger saplings can occupy a greater area, capture more solar radiation and thus have better chances of survival than small individuals losing to competition (Grossnickle, 2012). The more pronounced effect of decreased survival with decreasing initial plant size in *A. platanoides* may be due to interactive effects of the observed fungal co-infection detected, which also affects larger trees and thus dampens the effect of initial plant size.

Environmental variation was part of the main drivers of sapling mortality in FraDiv^{exp}, whereas van de Peer et al. (2016) found no effect of small-scale environmental variations on sapling survival in an afforestation experiment under homogeneous site conditions. The present study thus confirms that context dependency needs to be considered more explicitly when translating BEF designs into settings of enrichment plantings to reveal general BEF relationships in heterogeneous real-

world ecosystems.

Variables that have proven significant negative effects on mortality may, in turn, be considered indicators for overall tree survival. Soil pH was the only soil chemical parameter associated with sapling mortality in our study. Trends displayed by *T. cordata* and *F. excelsior* are in line with the environmental niche described for Central European forests with *T. cordata* also thriving on acidic soils while *F. excelsior* tends to prefer less acidic soil conditions (Leuschner and Ellenberg, 2017). Interestingly, mortality of *A. platanoides* was lowest at lower acidic conditions even though maple is known to tolerate but not to thrive in these conditions (Roloff and Pietzarka, 2014). This supports that consideration of not only soil conditions at the forest stand level but also small-scale variations within these forests can be critical to the success of replanting alternative tree species after the loss of ash.

Gap formation and increasing light intensity under the forest canopy is a direct effect of crown defoliation and loss of ash trees caused by ash dieback (Mitchell et al., 2016b). Canopy gaps can differ substantially in size and spatial arrangement depending on the initial abundance and spatial distribution of ash trees in the forest stand. Even though FraDiv^{exp} is located in forest stands severely affected by ash dieback, there are still several infected but living adult ash trees at each site contributing to heterogeneity including light availability. We found overall higher sapling mortality in areas of large canopy openness. In turn, it can be stated that tree survival and thus reforestation success may be higher, particularly in stands formerly dominated by ash that so far have only small gaps in the canopy. This could be an indication to address early replanting of trees once the ash tree fails.

The negative effect of increased light transmittance on the establishment of some temperate tree species might be an indirect one, as these conditions also favor the growth of competitive understory species such as bramble bush, grasses or forbs, thereby hindering tree and forest regeneration (Balandier et al., 2006; Gaudio et al., 2008). This is a particular challenge during forest transformation due to ash dieback: Jochner-Oette et al. (2021), for example, showed that grass coverage increased significantly with increasing gap fraction caused by ash dieback, which in turn led to a suppression of natural regeneration. Even though we found no overall effect of total herb layer cover on sapling mortality, species differed significantly in their reaction to high herb layer cover: mortality of *T. cordata* increased with rising herb layer cover, whereas mortality probabilities of *A. platanoides* decreased with increasing cover of the forest herb layer, which might indicate different responses to above- and belowground competition. In many experimental plots of these broken-up forest stands, multiple fast growing herbaceous species such as *Urtica dioica* L., *Galium aparine* L., *Impatiens* spp., and highly competitive grass species such as *Deschampsia cespitosa* (L.) P. Beauv. and others dominate the herb layer. Especially grasses and other graminoids with their extensive (often) lateral rooting system in the uppermost soil layer limit space and water availability and can thus prevent establishment of other species who are not able to reach lower soil layers yet (Balandier et al., 2006; Coll et al., 2003; Coll et al., 2004). Accordingly, Bloor et al. (2007) showed that ash seedling growth was limited by belowground competition for soil resources with grass.

Besides grass species and other graminoids, *Rubus* spp. are known to quickly colonize areas after forest canopy disturbance and they can hamper forest regeneration for many years by competing for natural resources like water, nutrients, and light (Mountford, 2006; Widen et al., 2018). Even though *Rubus* spp. was highly abundant in approximately two to three plots per site, we did not find an overall effect of *Rubus* spp. cover on sapling mortality. This might be explained by the repeated weeding. Lombaerde et al. (2021) found overall positive effects of understory removal on survival and growth of natural regeneration as well as planted seedlings and saplings. However, there were significant differences between the five tree species in the reaction to *Rubus* spp. cover. Surprisingly, only *A. platanoides* seemed to suffer at high proportion of *Rubus* spp. cover, whereas for all other tree species, this trend was reversed or not present at all. Increased mortality of maple at high cover

of *Rubus* spp. could be connected to the fungal infection. Microclimatic conditions during early summer in fast-growing bramble bush might have promoted fungal damage of maple saplings, before weeding in late summer, thus leading to higher mortality rates specifically in *A. platanoides*.

5. Conclusion

With an overall mortality of 5 %, FraDiv^{exp} was established as a BEF experiment in the midst of collapsing forests infected by ash dieback. Moreover, the overall low mortality of all species (except of maple) compared to other tree BEF experiments located on former arable land (e.g., Don et al., 2007; Yang et al., 2013), highlights the great advantage of establishing a tree BEF experiment within existing forest stands. First results on environmental variations and establishment success of FraDiv^{exp} reveal the complex processes and interactions in forest ecosystems infested by ash dieback. Context-dependent differences in species mortality underline the need to consider small-scale site heterogeneity when planning reforestations in formerly ash-rich forests. Nevertheless, one might deduce that tree survival in the system studied increases with increasing soil pH and that the probability of survival is higher the larger the initial size of the saplings and, above all, the denser the canopy. This could also lead to the recommendation to start replanting as early as possible while the canopy of a forest stand is not yet fully thinned. While pH and sapling height, and especially herbaceous layer and *Rubus* spp. cover, prove to be very good differential indicators of different survival probabilities among species (as indicated by significant covariate × species interactions), openness, i.e., denseness, is indeed a suitable overall indicator because it has a significant main effect across all species in the absence of interaction effects. Especially herb layer characteristics might determine which species might successfully serve as alternative tree species. In stands where the herb layer is already dominated by *Rubus* spp. and/or grassy species (as a consequence of canopy gaps and thus changed light regime due to progressing ash dieback), forest management need to take the species-specific sensitivity into account and particularly consider competitiveness of tree species in their juvenile stage. Within highly transformed forest sites, insensitive tree species need to be chosen to ensure reforestation. Moreover, at FraDiv^{exp}, we will analyze the performance of the trees in terms of growth and survival in relation to species identity, diversity levels and abundance and composition of plant and fungal communities on plot as well as individual level. At the same time, vascular plant and fungal diversity will be evaluated as the dependent variable, quantifying the ability of the five tree species to retain the high biodiversity characteristic for ash-dominated forests.

CRedit authorship contribution statement

Katharina S. Haupt: Investigation, Formal analysis, Writing – original draft. **Katharina Mausolf:** Investigation, Formal analysis, Writing – review & editing, Project administration. **Jessica Richter:** Investigation. **Joachim Schrautzer:** Conceptualization, Funding acquisition. **Alexandra Erfmeier:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing, Supervision.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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