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Vegetation responses to pathogen-induced tree loss: Swedish elm and ash forests revisited after 32 years

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Abstract Invasive fungal pathogens are an increasing problem globally and can cause strong effects on forest ecosystems. In this study, we contrast vegetation surveys in eutrophic elm (*Ulmus glabra*) and ash (*Fraxinus excelsior*) forests in southern Sweden, conducted just prior to the arrival of Dutch elm disease (DED) in 1989, and then again in 2021, several years after ash dieback (ADB) began. At the sample plot scale, species richness (α–diversity) of the upper tree layer strongly decreased from 1989 to 2021, and the mean cover of elm decreased from 27 to 1% and of ash from 29 to 13%. In the lower tree and shrub layers, elm and ash were replaced by other, mainly shade-tolerant, tree species. The cover and richness of the shrub layer increased in previously elm-dominated stands but not in ash-dominated stands. The extensive loss of canopy cover in elm stands caused a larger change in upper tree layer species composition and increased compositional variability (β-diversity) between plots when compared to the ash stands. The direction of the changes in tree layer composition between the surveys varied with soil moisture and nutrient availability. While beech increased in less eutrophic plots, more nutrient-rich plots changed toward hornbeam or small-leaved lime, and wetter plots turned toward alder and bird cherry. Hence, our results indicate increased compositional diversity and alternative successional pathways for community reorganization following DED and ADB. Future research will reveal if these pathways will later merge or further split.

Keywords Forest disturbance · *Hymenoscyphus fraxineus* · Long-term vegetation change · *Ophiostoma* sp. · Secondary forest succession · Temperate deciduous forest

Introduction

Since the early twentieth century, many of the world's temperate forests have been disturbed by introduced pests and pathogens (Lovett et al. 2006). Several of these introductions have resulted in the decline of foundation tree species which has far reaching impacts on forest ecosystem processes and biodiversity (Ellison et al. 2005).

Mortality of dominant or co-dominant tree species results in canopy openings of varying sizes, which promotes the immigration of woody and herbaceous plant species of varying shade tolerance. Hence, these disturbances have the potential to change the structure and diversity of the forest vegetation (Christensen et al. 2007; Peterken and Mountford 2017), and the trajectory and magnitude of vegetation changes may be expected to largely depend on the spatial scale of the disturbance (Pickett and White 1985).

In Europe, Dutch elm disease (DED), caused by fungal pathogens (*Ophiostoma* spp.) and spread by bark beetles (*Scolytus* spp.), brought about a widespread population decline of several elm species, including wych elm (*Ulmus glabra*, e.g., Thomas et al. 2018). More recently, European ash (*Fraxinus excelsior*) has also been affected by an emerging invasive fungal pathogen, *Hymenoscyphus fraxineus*, causing widespread ash dieback (ADB, e.g., Thomas 2016; Skovsgaard et al. 2017).

Old elm and ash trees provide valuable habitat for many associated species, including epiphytic bryophytes and lichens, fungi, and invertebrates of conservation concern and their loss has large impacts on ecosystem functioning and services (Mitchell et al. 2016; Thomas et al. 2018; Hultberg et al. 2020). Predicting the ecological impacts of novel changes to

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disturbance regimes requires a thorough understanding of the successional processes that follow these events, ideally based on long-term ecological studies (Hahn et al. 2007; Lindenmayer et al. 2010; Peterken and Mountford 2017). Unfortunately, only a few long-term case studies are available from European temperate broadleaf forests to provide detailed data on the changes in forest structure and composition that can be caused by fungal pathogens (Peterken and Mountford 1998, 2017; Brunet et al. 2014; Hytteborn et al. 2017; Kirby et al. 2014).

Here, we evaluate a resurvey of sample plots, conducted after 32 years (1989 and 2021) in 45 forest stands in southern Sweden affected by DED and ADB. Unlike previous case studies, our data thus provide a rare opportunity to evaluate forest development at a regional scale subsequent to two major pathogen-induced disturbance events. Specifically, we study how the dynamics of these sites have varied depending on previous dominance of elm or ash.

Even without the arrival of DED and ADB, one would expect successional changes to have occurred during the study period (Hahn et al. 2007). Although there are no unaffected sites left to demonstrate such non-pathogen-induced changes in the study region, evidence from the decades prior to the arrival of DED and ADB suggests that, in the absence of major disturbance events, the dominance of the shade-tolerant elm would have persisted or even increased in all canopy layers at the cost of the more light-demanding ash (Diekmann 1994; Brunet et al. 2014; Hytteborn et al. 2017).

We hypothesized that changes in abundance and diversity in the lower vegetation layers over time are driven by the degree of pathogen-induced canopy opening and related changes in light availability (Emborg 1998; Thomsen et al. 2005). Specifically, we investigated the following hypotheses: Losses of canopy cover due to DED and ADB have resulted in an establishment of other light-demanding species than ash as an effect of increased light availability (H1) or in an expansion of other shade-tolerant species than elm (H2), mainly from individuals already present in the stands (Christensen et al. 2007; Peterken and Mountford 2017).

In general, we expected these successional changes to be larger in elm-dominated plots than in ash-dominated as healthy elm canopies are denser than ash canopies and as DED started to affect the studied forests earlier than ADB and kills individual trees more rapidly. As a result of these differences, we also expected an increase in overall species turnover between plots (beta-diversity).

Materials and methods

Study region and original forest types

Skåne is the southernmost province of Sweden (area 11,300 km^2, central coordinates WGS84: 55.94042 N, 13.53669 E) and has a temperate/subhumid climate with an annual precipitation of 600–900 mm and mean monthly temperatures ranging from − 1 °C in January to 18 °C in July (period 1991–2020, www.smhi.se). The natural forest vegetation is characterized by temperate broadleaf forests (Leuschner and Ellenberg 2017). On the most productive soils in southern Sweden, forest communities dominated by ash and elm can be found (Diekmann 1994, 1999). Prior to DED and ADB, these forests covered ca 5000 ha (1.5% of the forest area) in the study region (SLU 2000), mainly on steep slopes and in various sites characterized by their high soil moisture, e.g., along streams. Most stands are multi-layered, with hazel (*Corylus avellana*), bird cherry (*Prunus padus*), and hawthorn (*Crataegus* spp.) being the most common species of the shrub layer and with a diverse herbaceous layer of nutrient-demanding and calcicolous species (Brunet 1991).

Original vegetation survey 1988–1990

During the years 1988–1990 (from here on the 1989 inventory), 94 vegetation plots (size range 10 × 10 to 20 × 20 m) were surveyed within forest patches located throughout Skåne that were dominated by wych elm and/or European ash (Brunet 1991). Such patches were identified with information from a regional forest inventory containing data on forest patch size, age, and tree composition. In general, sample plots were located in the central parts of forest patches with a stand age of at least 60 years and a relatively closed tree canopy. Most stands historically developed on former wooded meadows of coppice type (Diekmann 1999). A particularly aggressive strain of DED (*Ophiostoma novo-ulmi*) was first recorded in 1979 (Persson 1987), and DED started to spread across the province during the late 1980s. The 1989 inventory was thus conducted just prior to extensive losses of wych elm due to DED. Ash dieback was first recorded in the region in 2001, and serious damage by ADB started to appear over subsequent years (Stener 2018).

Resurvey 2021

In April and May 2021, 67 different forest patches were visited to assess the possibility to relocate vegetation plots of the 1989 inventory. Plot relocation was based on information provided in the original sample protocols. Geographical coordinates were extracted in 1988–1990 from the topographical map to an accuracy of 50 m. In 2021 the original plot locations were searched using a handheld GPS and specific protocol information on location, slope inclination and cardinal direction, the species composition of the tree layer and the original occurrence of certain, and rare herbaceous plant taxa. Considering this approach, the plots can be regarded as quasi-permanent, as the resurvey plots are located in the same forest patch as the original plots, but with a varying degree of direct overlap with the original plot location (Kapfer et al. 2017). Forest patches were excluded if the degree of disturbance obstructed the relocation of sample plots. Such disturbance mainly consisted of clearcutting and replanting.

In April and May 2021 (spring ephemerals in the ground layer) and July and August 2021, species composition and cover was resurveyed in 54 relocated sample plots in 45 different forest patches, using the 1989 inventory methodology (Brunet 1991, Online Table A3). Overall cover percentage of the upper tree layer (UT, > 20 m height), the lower tree layer (LT, 6–20 m), the shrub layer (S, 1–6 m), and the ground layer (G, 0–1 m) was visually estimated in each plot (Online Table A3). Complete lists of plant species were compiled and the cover of individual species in each of these four vegetation layers was estimated using a six-degree cover class scale (+, < 1%; 1, 1–5%; 2, 6–25%; 3, 26–50%; 4, 51–75%; 5, 76–100%; Online Tables A4 and A5). For data analysis, cover class "+" was transformed to 0.5%, and arithmetic means of cover were used for cover classes 1 to 5 (3, 15, 38, 63, 88%). As ground layer data included both spring ephemerals and summer species, total cover often exceeded 100%.

In 46 plots, no traces of recent forest management were observed, while sanitary cutting, but not replanting, had been done to a varying degree in eight plots. In 2021, 26 of the plots occurred within nature reserves and 12 plots occurred within registered woodland key habitats (Online Table A3).

Data analysis

For statistical analyses, which all were done in R version 4.1.2 (R Core Team 2021), the dataset was classified into elm-dominated plots with an initial cover of wych elm of more than 25% in the upper tree layer (cover classes 3–5), and/or at least 50% in the lower tree layer (cover classes 4–5, $n = 27$, elm dominance), and other plots with lower initial cover of elm (less than 25%, cover classes 1 or 2) in the tree layers where ash was the most important canopy species ($n = 27$, ash dominance), respectively.

We used Generalized Linear Mixed Models (GLMM) to model the effects of time and initial elm dominance on the total species richness and total plant cover of the four vegetation layers. The model was built with a factorial variable with eight levels (one for each combination of layer and initial elm/ash dominance), a factorial variable with two levels (one for each inventory), and the interaction between these two variables. The model thus resulted in an individual intercept and time effect for each of the eight combinations of layer and initial elm dominance. These models were built with the glmmTMB function in the glmmTMB package (Brooks et al. 2017) with plot as a random intercept effect. The species richness was modeled with a Conway–Maxwell–Poisson distribution and log link, while the cover model used a beta-distribution and logit link. The cover model also included a dispersion model, with the same explanatory variables as the conditional model, to account for heteroscedasticity. The models were evaluated by the simulateResiduals function in the DHARMa package (Hartig 2021).

Wilcoxon signed-rank tests were applied to analyze the effects of time and initial elm or ash dominance on cover of elm and ash, respectively, and on cover of two groups of other trees and tall growing shrubs (potential height ≥ 6 m) with high and low shade traits, respectively. Late successional species with high to very high shade cast and shade tolerance, and early successional species with very low to moderate shade cast and shade tolerance according to Leuschner and Ellenberg (2017) were assigned to these two different groups (excluding ash and elm, see Online Table A1 for details). Wilcoxon tests were performed with the wilcoxsign_test function in the coin package (Hothorn et al. 2006). As seedling abundance of tree species shows high inter-annual variation, these tests were not performed for the ground layer. Mean P-values and their 99% confidence intervals were calculated from Monte Carlo resampling and zeros were handled by the "Pratt" method (Pratt 1959).

Multivariate analyses were performed on the plant community data (cover) of the four vegetation layers separately, excluding the plots which did not have any plant cover in one or both of the inventories in that specific layer. Non-metric Multidimensional Scaling (NMDS) was performed on the layers separately, and depending on the layer assessed, two or three dimensions were required to reduce the stress level (stress = 0.17–0.20) to acceptable levels. We calculated community-weighted indicator (CWI) values for soil moisture and nutrient availability based on the cover data of the ground vegetation and Tyler's indicator values (Tyler et al. 2021). Let c_{ij} be the cover % of species i in sample plot j, and x_i be the indicator value of species i. To estimate the value of soil moisture and nutrient availability, a weighted average of all values of those species present in the plot was calculated according to the following formula (Diekmann 2003):

$$\mathrm{CWI} = \sum_{i=1}^{n} \left(c_{ij} * x_i\right) \Big/ \sum_{i=1}^{n} c_{ij}.$$

The resulting weighted indicator values (Online Table A5) were then fitted as vectors to the NMDS of the upper and lower tree layers (envfit).

To test for differences in composition between the two inventories within the stands that were elm- or ash-dominated at the first inventory, we did permutational Multivariate Analysis of Variance (perMANOVA, Anderson 2001), with time (the two inventories), elm or ash dominance (two levels), and their interaction, as explanatory variables. If the interaction was significant ($P < 0.05$), this was followed by a pairwise perMANOVA to test for the specific effect of time within plots previously dominated by elm or ash. Additionally, we tested for differences in beta-diversity between the two inventories, within the stands with elm or ash dominance at the first inventory. This was done by permutation tests for homogeneity of multivariate dispersions (PERMDISP, Anderson 2006) followed by pairwise comparisons of the two inventories within dominance class. A PERMDISP is a distance-based test that uses principal coordinate axes to estimate the dispersion in multidimensional space. The distance to its centroid of a point is

$$z_{ij}^{c} = \sqrt{\Delta^2\left(u_{ij}^{+}, c_i^{+}\right) - \Delta^2\left(u_{ij}^{-}, c_i^{-}\right)},$$

where Δ^2 is the squared Euclidean distance between u_{ij}, the principal coordinate for the jth point in the ith group, and c_i is the coordinate of the centroid for the ith group. For more details, see Anderson (2006) and Oksanen et al. (2022).

The PERMDISP tests were run with an explanatory variable with four levels indicating the inventory and whether a plot initially was dominated by elm or ash. All multivariate analyses were done with Bray–Curtis distance and 9999 permutations constrained within plot. The NMDS, perMANOVA, and the PERMDISP tests were conducted using the metaMDS/envfit, adonis2, and betadisper/permutest functions, respectively, all within the vegan package (Oksanen et al. 2022).

Results

Changes in species cover

Cover in the upper tree layer decreased across all plots between 1989 and 2021, while between-plot variation increased (Table 1). Initial elm dominance was associated to a greater loss of cover (Δ47% cover, Table 1) than initial ash dominance (Δ25%). In plots with initial elm dominance, there was a clear increase in cover of the shrub layer. In contrast, there was a general but only slight decrease in ground layer cover.

Species richness decreased in the upper tree layer and increased in the shrub layer, respectively, in plots dominated by elm in 1989. However, in plots with initial ash dominance, species richness of the ground layer decreased between 1989 and 2021 (Table 1).

No elm trees survived in the upper tree layer in plots previously dominated by elm, while some single elm trees had survived in the upper tree layer of initially ash-dominated plots (Table 2). The cover of elm also strongly decreased in the lower tree layer of what were previously elm-dominated plots. In both plot groups, ash has lost around half of its original cover in the upper tree layer (Table 2), and also decreased in cover in the lower tree layer of plots previously dominated by ash (Table 2).

In plots initially dominated by elm, woody species with high shade traits increased their cover in all layers (supporting hypothesis 2, H2), while the cover of species with low shade traits only increased in the shrub layer between 1989 and 2021 (partly supporting H1, Table 2). In plots with initial ash dominance, species with high shade traits increased their cover in the lower tree and shrub layers, while cover

Table 1 Mean cover and species richness (SD in parentheses) in four vegetation layers in 1989 and 2021 in sample plots with initial ash ($n = 27$) or elm dominance ($n = 27$), respectively

	Ash dom. 1989			Elm dom. 1989		
	1989	2021	*P*	1989	2021	*P*
Mean cover (%)						
Upper tree layer	76 (11)	51 (21)	**< 0.001**	78 (11)	31 (29)	**< 0.001**
Lower tree layer	21 (19)	26 (17)	0.718	30 (23)	29 (25)	0.940
Shrub layer	27 (25)	30 (20)	0.567	19 (15)	31 (21)	**0.006**
Ground layer	163 (39)	144 (37)	**0.016**	162 (43)	146 (40)	**0.041**
Species richness						
Upper tree layer	2.9 (1.5)	2.5 (1.2)	0.300	2.5 (1.0)	1.5 (1.1)	**0.004**
Lower tree layer	2.7 (1.5)	2.7 (1.1)	0.930	1.8 (0.9)	2.1 (1.4)	0.322
Shrub layer	4.8 (2.1)	4.9 (2.3)	0.886	3.4 (1.7)	5.1 (2.1)	**< 0.001**
Ground layer	27.5 (7.4)	24.6 (6.5)	**0.009**	19.3 (4.3)	20.6 (5.7)	0.162

P-values according to GLMM. $P < 0.05$ in bold face

Table 2 Mean cover % (SD in parentheses) of elm, ash, and other high and low shade woody species, respectively

Species	Ash dom. 1989			Elm dom. 1989		
	1989	2021	*P*	1989	2021	*P*
Ulmus glabra UT	4 (7)	1 (4)	**0.041**	50 (20)	0 (0)	**< 0.001**
Ulmus glabra LT	4 (8)	6 (9)	0.559	19 (20)	5 (7)	**0.008**
Ulmus glabra S	2 (5)	3 (8)	0.091	9 (9)	10 (12)	0.859
Fraxinus excelsior UT	40 (23)	18 (17)	**< 0.001**	17 (20)	8 (11)	**0.005**
Fraxinus excelsior LT	4 (6)	1 (3)	**0.004**	1 (4)	4 (13)	0.861
Fraxinus excelsior S	3 (5)	1 (1)	0.087	0 (1)	1 (1)	0.337
High shade species UT	13 (16)	18 (23)	0.090	13 (15)	20 (23)	**0.041**
High shade species LT	12 (19)	15 (17)	**0.036**	8 (13)	21 (24)	**< 0.001**
High shade species S	2 (3)	6 (10)	**0.027**	3 (5)	8 (11)	**< 0.001**
Low shade species UT	13 (18)	15 (19)	0.595	2 (8)	1 (4)	0.753
Low shade species LT	6 (11)	11 (17)	0.159	1 (7)	3 (12)	0.126
Low shade species S	19 (22)	20 (20)	0.222	7 (12)	12 (16)	**0.018**

Values are shown for the three canopy layers, as surveyed in both 1989 and 2021 for sample plots with a low and high initial canopy cover of elm in the tree layer, respectively. Mean *P*-values according to Wilcoxon signed-rank tests and Monte Carlo simulations (see Online Table A2 for confidence intervals of mean *P*-values). $P < 0.05$ in bold face. Canopy layers, *UT* upper tree layer, *LT* lower tree layer, *S* shrub layer

of species with low shade traits did not increase in any layer (supporting H2, Table 2).

Changes in species composition

Species composition generally differed between the inventories in all layers ($P < 0.001$–0.005) and between plots with initial elm or ash dominance ($P < 0.001$–0.039, $P = 0.069$ for the lower tree layer) according to the perMANOVAs. It was however only in the case of the upper ($P < 0.001$) and lower tree layer ($P = 0.013$) that the interaction between time and initial elm or ash dominance was significant. The pairwise perMANOVA revealed significant changes in species composition of the upper and lower tree layers independently if the plots were previously elm-dominated ($P < 0.001$, $P = 0.026$) or ash-dominated ($P = 0.004$, $P = 0.002$). This effect was, however, much stronger in the elm-dominated ($R^2 = 0.27$, $R^2 = 0.04$) than ash-dominated ($R^2 = 0.07$, $R^2 = 0.02$) plots.

The PERMDISP test showed significant ($P < 0.001$) differences in beta-diversity in the upper tree layer among the four categories, and the pairwise comparison revealed that the beta-diversity had changed over time both in plots with elm ($P < 0.001$) and ash dominance ($P = 0.002$). In both cases, beta-diversity had increased over time, but as indicated by the change in average distances to the medians in ordination space, the change was larger in plots that were initially elm-dominated (Δ0.26) than in those that were ash-dominated (Δ0.16), which was according to our expectation. The overall PERMDISP tests were not statistically significant for any of the other layers ($P = 0.141$–0.168). The pairwise comparisons revealed however a significant ($P = 0.007$) increase over time (Δ0.05) in the ground layer of the elm-dominated plots, but not in the ash-dominated plots ($P = 0.186$, Δ0.02).

According to the NMDS analyses, the species composition clearly differed between plots with initial elm and ash dominance in all layers except the lower tree layer (Fig. 1). In all layers except the lower tree layer, the centroids of the initially elm-dominated plots were located closer to those of the ash-dominated plots, and there were larger compositional overlaps, in the second inventory than in the first (Fig. 1). Changes in composition between inventories for the upper and lower tree layers varied with soil conditions, as indicated by the CWIs for soil moisture and nutrient availability (Fig. 2).

Comparisons of the two plot types showed that elm-dominated plots had significantly ($P < 0.05$) lower mean ecological indicator values for soil moisture (5.0 ± 0.3 sd in both surveys) than ash-dominated plots (5.5 ± 0.6 sd in both surveys), while nutrient indicator values did not differ between surveys or plot types (6.4–6.5 ± 0.2 sd, ANOVA, and Tukey tests).

Discussion

Changes in species cover

Our results show that the cover loss of elm from the upper and lower tree layers between the survey periods (50 and 14%, respectively) is much greater than that of ash (22 and 3%), which is partly explained by the fact that DED arrived in the study region about 20 years earlier than ADB. Elm

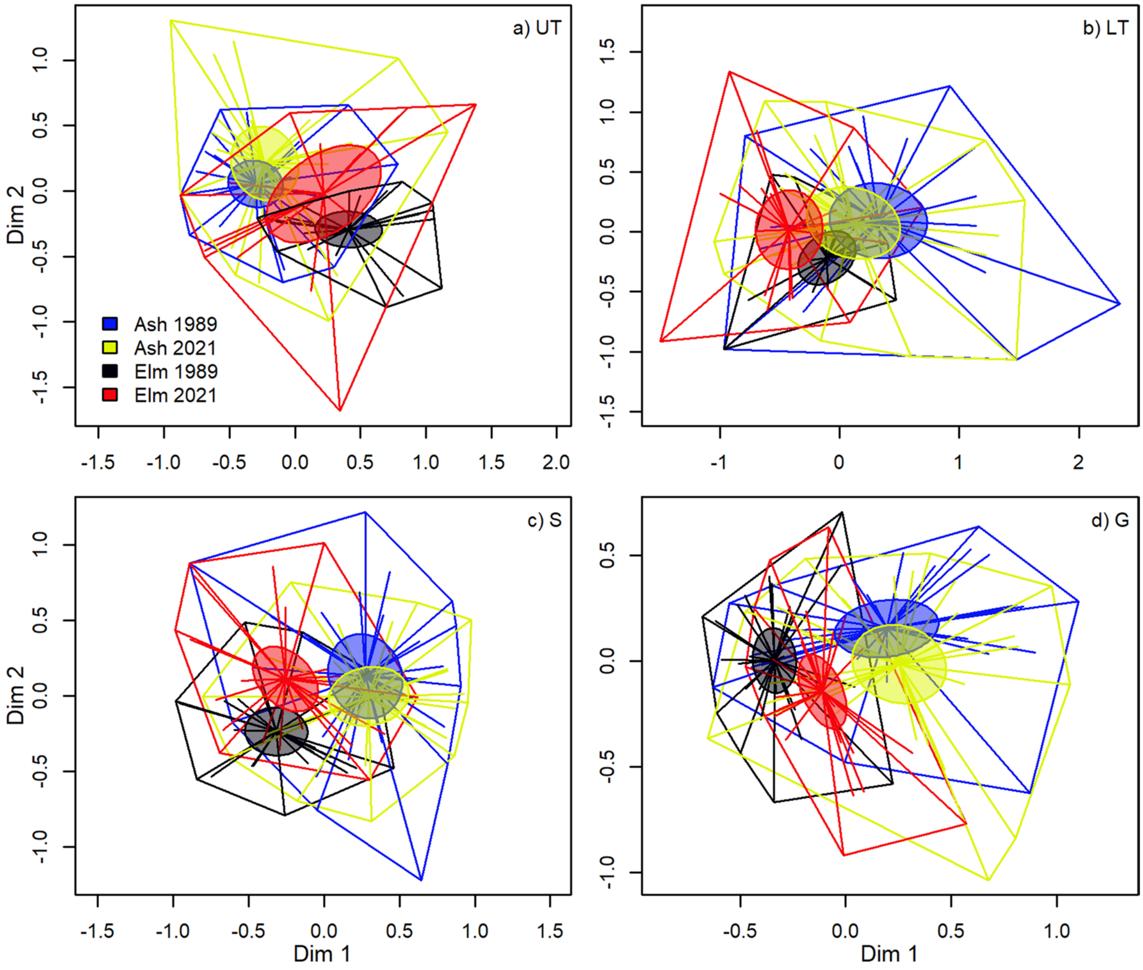

Fig. 1 Ordination diagrams of Non-Metric Multidimensional Scaling of the plant communities in the **a** upper tree (UT), **b** lower tree (LT), **c** shrub (S), and **d** ground (G) layers for initially elm- or ash-dominated plots. The outer lines show the total distribution of the samples in ordination space, while the lines from the samples' centroids show the position of the individual plots per inventory. Ellipsoids are 95% confidence intervals

has almost completely disappeared from the upper tree canopy across all plots studied. Only a few single larger elm individuals remain alive in a small number of plots initially dominated by ash, possibly protected from infection by lack of root contact with other elm trees and not yet detected by the beetle vectors (Thomas et al. 2018). Elm still maintained its cover in the shrub layer which is in accordance with previous observations on young elm persisting in the woody understory (Brunet et al. 2014; Hytteborn et al. 2017; Peterken and Mountford 2017). However, elm trees tend to be infected once their trunk diameter exceeds 10 cm. Fortunately, for the species long-term survival, seed production can usually begin several years before individual stems reach this size (Thomas et al. 2018).

The large-scale loss of elm cover from the tree layers in elm-dominated plots has resulted in a clear expansion of other species in all woody layers in terms of both cover and species richness. However, the expansion in ash-dominated plots was less pronounced which is probably explained by the more recent disturbance and the smaller cover loss of ash in the tree layers so far. Resurvey studies have shown increasing mortality rates with time, but also a small share of ash relatively tolerant to ADB (Thomas 2016; Stener 2018; Matisone et al. 2021). For potential development of tolerance to ADB, it is therefore important not to clear-cut affected stands, but to retain living ash trees with low damage levels (Rosenvald et al. 2015; Skovsgaard et al. 2017).

Changes in species composition

The ordination analyses showed that the relatively larger loss of canopy cover in the elm plots caused both a larger overall change in species composition and an increasing compositional variability (β-diversity) between plots when compared to the ash plots. The release of the community from elm losing its status as the canopy dominant triggered

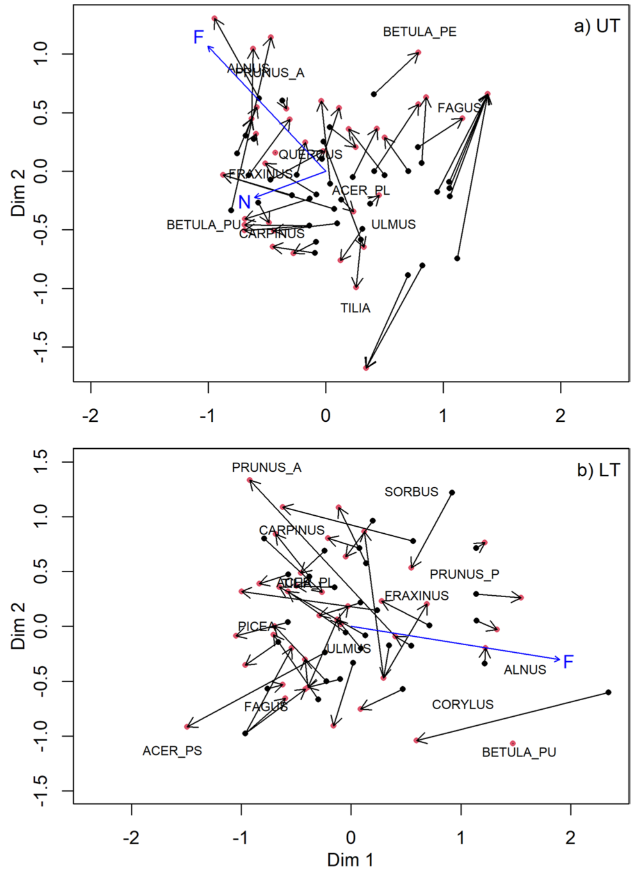

Fig. 2 The position of species (see Online Table A1 for species codes) and of plot pairs in ordination space from Non-Metric Multidimensional Scaling of the species communities in the **a** upper and **b** lower tree layers (for which the perMANOVAs indicated interactive effects of tree species and time on community composition) in the initial (black dots) and final (red dots) surveys. Black arrows between plots show the direction of change between surveys, while blue arrows show the fitted vectors of community-weighted mean indicator values for soil moisture (F) and nutrient availability (N)

a rather diverse set of secondary successions partly controlled by interactions with soil moisture, nutrient availability, and tree species ecology. Nevertheless, the elm plots also became compositionally more similar to the ash plots across the vegetation layers, probably as an effect of overall lower variability in light conditions as the dense elm-dominated canopies were absent in 2021.

As a result of the loss of elm and ash at our study sites, other tree species have now taken advantage of the new growing space by increasing in abundance. However, these increases have not yet filled the canopy gaps after DED and ADB in the upper tree layer This may reflect the limited time available for post-disturbance recovery, as well as the relatively low initial abundance of most other tree species, as elm and ash are the two most competitive tree species at moist and eutrophic sites in southern Sweden (Diekmann 1994, 1999). How fast other tree species can fill the canopy gaps caused by DED and ADB will likely depend on the local prevalence of tree species, as well as on life-history traits. These traits include growth patterns, seed production, and dispersal, which can interact with abiotic and biotic factors, such as soil conditions, ground vegetation, and ungulate browsing (Leuschner and Ellenberg 2017; Peterken and Mountford 2017; Skovsgaard et al. 2017).

Differences in the ecology and physiognomy of the local tree species pool will probably result in relatively long-lasting differences in canopy structure. In our study, less nutrient-rich plots changed toward a higher share of beech (*Fagus sylvatica*), whereas more nutrient-rich plots changed toward hornbeam (*Carpinus betulus*) or small-leaved lime (*Tilia cordata*). Likewise, wetter plots turned toward a higher share of black alder (*Alnus glutinosa*) and bird cherry. A similar spatial heterogeneity in compositional change was observed in permanent plots with ash in Latvia after 15 years (Matisone et al. 2021).

Strengths and weaknesses in vegetation resurvey studies

Stand-structural attributes are widely used in forest ecology as a measure of light availability (Angelini et al. 2015). Depauw et al. (2021) showed in forests similar to those in our study that estimated canopy cover was a better predictor of mean indicator values for light than basal area or canopy closure (from a spherical densiometer). However, unlike repeated inventories of trees and their size or age, cover estimates may not provide information on population changes. For example, a decrease in overall cover due to mortality of large trees may, or may not, be correlated with a decrease in stem numbers (Peterken and Mountford 1998).

The main focus of our study was, however, to analyze the effects of canopy cover loss on vegetation dynamics. Visual cover estimates are prone to three types of observer error: (a) overlooking species, (b) inaccurate species identification, and (c) inaccurate abundance estimates (Milberg et al. 2008; Morrison 2016). The large size of our sample plots motivated the use of broad cover classes which reduced the importance of the latter error source (Morrison 2016). During resampling, additional sources of error include inaccurate plot relocation, observer bias, and seasonality bias (Kapfer et al. 2017; Verheyen et al. 2018). Non-permanent vegetation plots can be divided into quasi-permanent (approximate relocation) and non-traceable (random relocation within a sampled area) plots, and relocation errors may be non-negligible when resurveying quasi-permanent plots (Milberg et al. 2008; Verheyen et al. 2018).

To reduce the inherent sources of error in our study, we (a) only resurveyed historical vegetation plots with information on approximate plot location, (b) considered other information available from the original survey to minimize relocation errors, and (c) resurveyed at times of the year when vegetation development was comparable to the original survey (Kapfer et al. 2017). Most importantly, all field work in both surveys was done by the same person (the first author), removing between-observer bias.

We did not quantify and report the relocation error by comparing alternative resurvey plots in a subset of the data (Verheyen et al. 2018). However, Kopecký and Macek (2015) have demonstrated that the resurvey of quasi-permanent plots can provide vegetation change assessment comparable to permanent plots, as long as the following information is combined for plot relocation: geographic coordinates extracted from historical maps, local topography, and species composition of the tree layer. In our study, we used all three sources and information on rare plant species in the ground layer.

Successional processes in unmanaged forests

Despite the presence of disease-induced canopy gaps of varying size in many of our plots, colonization by shade-intolerant early successional tree species such as European aspen (*Populus tremula*) and birches (*Betula pendula, B. pubescens*) was almost absent (cf. Online Table A1). This is in contrast to findings from Lithuania, where regeneration of birch, aspen, and grey alder (*Alnus incana*) was abundant in damaged ash stands (Lygis et al. 2014). However, the sites studied in Lithuania were open clear-cuts after salvage logging and with higher light flux and more disturbed ground, while our study sites remained mostly unmanaged with prevalent shading by trees and shrubs. Correspondingly, canopy recovery in our plots was characterized by shade-tolerant late successional tree species (beech, hornbeam, maples) and moderately shade-tolerant mid-successional bird cherry and hazel. The latter two were part of the low shade species group in our analyses, which explains the increase in cover of this group in the shrub layer of the previously elm-dominated plots. Especially in the previously ash-dominated plots this increase in shade-tolerant tree species implies a functional shift which, even without healthy elm as the main driver, may in the long run decrease light influx and affect ecosystem processes. A similar succession was observed in a broadleaf forest reserve dominated by elm and ash in central Sweden, where all of the large elms had died from DED between 2000 and 2010 (Hytteborn et al. 2017). In response, there was an increase bird cherry, hazel, Norway maple (*Acer platanoides*), and young elm. Notably, ash also increased its abundance in response to competitive release from elm by DED in several long-term studies in the UK and Sweden prior to the arrival of ADB (Brunet et al. 2014; Hytteborn et al. 2017; Kirby et al. 2014; Peterken and Mountford 2017).

In the mainly unmanaged forests of our study, several processes may act simultaneously during succession after DED and ADB. First, larger individual trees (beech, maple, hornbeam, lime, oak) that are already established expand their crowns into the new gaps (Christensen et al. 2007). Second, species with the ability to produce root sprouts and adventitious shoots may effectively expand into gaps (Peterken and Mountford 2017). In our plots, hazel and bird cherry were frequently observed to follow this strategy (see also Matisone et al. 2021), as did black alder and small-leaved lime on occasion. Third, existing saplings and advanced regeneration of shade-tolerant trees are released from competition and increase their growth rates (Christensen et al. 2007). For example, ingrowth from the advanced regeneration of beech and Norway maple was relatively common in our study, and hornbeam and sycamore (*Acer pseudoplatanus*) responded likewise (Online Table A1). Whereas sycamore is introduced in Sweden and relatively uncommon, when locally present it often forms dense carpets of saplings in the ground layer which can rapidly develop into pure young stands after canopy disturbance (Felton et al. 2013), as was the case in two of our plots.

The cover (both ash and elm plots) and species richness (ash plots) of the ground vegetation were slightly lower in 2021, which was unexpected as an overall lower canopy cover should favor growth of ground layer species. More detailed analyses are required to explain these changes, which may be driven by a range of factors including inter-annual climatic variation (e.g., drought, Peterken and Mountford 2017; Brunet and Tyler 2000), more intensive herbivory (von Oheimb and Brunet 2007; Brunet et al. 2016) or interactions between ground vegetation and the changing shrub layer.

In conclusion, our results show that succession may take multiple alternative pathways for community reorganization following the loss of elm and ash, leading to increased β-diversity. Whether these pathways will later merge or further split is a question for future research. Further research is also needed to investigate the impact of these pathogen-induced disturbances on the composition and diversity of other taxonomic groups, connected to the vegetation changes observed here, or more directly to ash and elm.

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Author contributions JB and AF developed the concept of the resurvey project. JB collected the field data in 1988–1990 and 2021. POH and JB analyzed the data. JB, AF, and POH wrote the manuscript.

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Data availability The raw data can be found in the Online tables A3-5 in the Supplementary Information.

Declarations

Conflict of interest The authors of this paper have no conflict of interest to declare.

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