

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 devastating 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.

Mean cover and species richness (α -diversity) of the upper tree layer strongly decreased from 1989 to 2021. In the lower tree layer, loss of elm and ash was compensated by an increase in other tree species. The cover and richness of the shrub layer increased in previously elm-dominated stands but not in ash-dominated stands. Canopy recovery was mainly dominated by shade-tolerant tree species which, especially in the previously ash-dominated stands, implies a successional shift.

The extensive loss of canopy cover in elm stands caused a larger change in 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 towards hornbeam or small-leaved lime, and wetter plots turned towards 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.

Introduction

Since the early 20th 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). Exotic pests and pathogens often produce more long-lasting changes to tree species composition than abiotic disturbances such as wind or fire. This is because these pests and pathogens remain as permanent components of the forest ecosystem and continuously affect their non-adapted host tree species (Lovett et al. 2006).

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 diversity of the forest vegetation (Smith et al. 2009) and the trajectory and magnitude of vegetation changes may be expected to be largely dependent of the scale of the disturbance (De Frenne et al. 2013).

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*, 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, Pautasso et al. 2013, Thomas 2016).

Elm and ash are highly valued for their timber, as well as for their biodiversity and amenity values (Thomas 2016, Thomas et al. 2018). Old elm and ash trees provide valuable habitat for many associated species, including epiphytic bryophytes and lichens, fungi and invertebrates of conservation concern (Mitchell et al. 2014, 2016, 2017, Thomas et al. 2018, Hultberg et al. 2020). Elm and ash also share a large number of associated species, which makes the almost simultaneous loss of both tree species particularly severe from a conservation point of view (Mitchell et al. 2017, Hultberg et al. 2020).

The successful breeding of genotypes that are resistant to the pathogenic fungi is an ongoing challenge (Martin et al. 2019, 2021, Stener 2018, Plumb et al. 2019, Stocks et al. 2019). Meanwhile, forest recovery and maintenance of ecosystem function and biodiversity will have to rely on other tree species, either as a result of natural succession or active management (Mitchell et al. 2016, 2017, Skovsgaard et al. 2017).

Predicting the ecological impacts of changing disturbance regimes requires a thorough understanding of the successional processes that follow these events; ideally based on long-term ecological studies (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.

Using data from six tree inventories, Peterken and Mountford (1998, 2017) followed a population of wych elm in Lady Park wood, an English woodland reserve, from 1950 to 2013. In 1992, about 65% of the elms that were present 42 years ago, had been killed by DED, but the elm population had actually increased by 40% through seedling regeneration and stump regrowth from the base of old trees. After 1992, however, this increase in density was followed by a massive decrease and steadily increasing mortality of young trees by DED until 2013. The authors conclude that the prolific regeneration recorded until 1992 probably had been based on a final shower of seed from dying canopy trees and shoots from still-vigorous root systems (Peterken and Mountford 2017).

Two case studies from mixed broadleaf forest reserves in Sweden (Dalby Söderskog and Vårdsätra) showed a similar pattern with almost complete losses of large elms, but young elm still persisting in the woody understory, although with increasing mortality of such young trees as well (Brunet et al. 2014, Hytteborn et al. 2017). As a response to competitive release from elm by DED, ash increased its abundance in both forests until the arrival of ADB. Other woody species with more persistent increases included Norway maple (*Acer platanoides*), hazel (*Corylus avellana*), beech (*Fagus sylvatica*) and bird cherry (*Prunus padus*, Brunet et al. 2014, Hytteborn et al. 2017). Kirby et al. (2014) also reported an increase of ash in the English forest reserve Wytham woods since 1974 and argue that the species most likely to increase, in case of severe ADB, would be Sycamore (*Acer pseudoplatanus*), hazel and pedunculate oak (*Quercus robur*). Also in the old-growth parts of Lady Park wood, the basal area of ash had steadily increased since 1945 and in 2010 ash ranked second after beech. ADB had not yet arrived to

the forest at the time, but in case of severe dieback, ash may be mainly replaced by beech, oaks (*Quercus* spp.) and limes (*Tilia* spp., Peterken and Mountford 2017).

The objective of this study was to increase our knowledge concerning how DED and ADB affect the structure and composition of temperate broadleaf forests, based on a re-survey of (quasi)-permanent sample plots, done after 32 years (1989 and 2021) in 45 forest stands in southern Sweden. 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, and thus highly targeted, disturbance events. We expect that these pathogens have instigated distinct shifts in forest plant species diversity and composition.

Specifically, we study how the successional trajectories of these sites have varied depending on previous dominance of elm or ash and hypothesize that the changes in composition and diversity in the lower vegetation layers over time are driven by the degree of pathogen induced canopy opening. As healthy elm casts more shade than healthy ash and DED started to affect the studied forests earlier than ADB, we expect larger vegetation changes in previously elm-dominated sample plots.

Material And Methods

Study region and original forest types

Skåne is the southernmost province of Sweden (area 11300 km², central coordinates WGS84: 55.94042N, 13.53669E) 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 broadleaf forests belonging to the order Fagetalia sylvaticae (Leuschner and Ellenberg 2017). On the most productive soils in southern Sweden, forest communities of the alliances Alno-Ulmion and Tilio-Acerion can be found (Diekmann 1994, 1999, Leuschner and Ellenberg 2017). At present, these forests only occur over small areas, as most suitable sites have been converted to crop fields in the past. Small remnant stands have survived on steep slopes (Tilio-Acerion) and in various sites characterized by their high soil moisture, e.g. along streams (Alno-Ulmion). Prior to pathogen-induced tree decline, forest communities of both alliances frequently had a tree layer dominated by European ash and/or wych elm, often with some admixture of other broadleaf tree species (Brunet 1991, Diekmann 1994, 1999). The herbaceous layer of these forests is rich in nutrient-demanding and calcicolous species, including spring ephemerals (*Allium ursinum*, *Anemone nemorosa*, *A. ranunculoides*, *Corydalis cava*, *Ficaria verna*, *Gagea lutea*), and shade-tolerant summergreen herbs (*Aegopodium podagraria*, *Campanula latifolia*, *Lamium galeobdolon*, *Mercurialis perennis*, *Polygonatum multiflorum*). Most stands are multi-layered, with hazel (*Corylus avellana*), bird cherry (*Prunus padus*) and hawthorn (*Crataegus* spp.) as the most common species of the shrub layer (Brunet 1991). In addition to their species-rich vascular plant flora, old-growth stands of these forest types are of high conservation value, due to their rich assemblages of bryophytes, lichens, soil fungi,

invertebrates and birds (Pautasso et al. 2013, Mitchell et al. 2017, Thomas et al. 2018, Hultberg et al. 2020).

Original vegetation survey 1988–1990

During the years 1988–1990 (from here on the 1989 inventory), vegetation plots (size range 10x10 to 20x20 m) were surveyed within forest patches located throughout Skåne, that either contained or were dominated by wych elm and/or European ash (Brunet 1991). 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 original survey 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).

Re-survey 2021

In April and May 2021, 67 different forest patches were visited to assess the possibility to relocate vegetation plots of the original survey. 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 hand held GPS and specific protocol information on location, slope inclination and cardinal direction, and the original occurrence of certain, rare herbaceous plant taxa. Considering this approach, the plots can be regarded as quasi-permanent, as the re-survey 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.

In April and May 2021 (spring ephemerals in the ground layer), and July and August 2021, species composition and cover was re-surveyed in 54 relocated sample plots in 45 different forest patches, using the original survey methodology (Brunet 1991). 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. Complete lists of plant species were compiled and the cover of individual species in each of these four vegetation layers was estimated by using the six-degree Braun-Blanquet scale (+, 1–5, Leuschner and Ellenberg 2017). 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 green 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, 27 of the plots occurred within nature reserves or habitat protection areas, and 11 plots occurred within registered woodland key habitats. Both surveys were carried out by the same surveyor.

Data Analysis

For statistical analyses, which all were done in R version 4.1.2 (R Core Team 2021), the data set 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), and 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 modelled 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 $\geq 6\text{m}$) 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 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).

All the multivariate statistical methods described below were performed on the plant community data (cover) of the four vegetation layers separately. Prior to analyzes, plots which did not have any plant cover in one or both of the inventories in a layer were excluded from the analyzes of 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). These indicator values 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), 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) followed by pairwise comparisons of the two inventories within dominance class. 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 analyzes 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

Canopy cover in the upper tree layer decreased across all plots between 1989 and 2021, initial elm dominance was associated to a greater loss of cover ($\Delta 47\%$ cover, Table 1) than in ash stands ($\Delta 25\%$). In plots with initial elm dominance, there was a clear increase in cover of the shrub layer. There was a general but only slight decrease in ground layer cover.

Table 1. Mean cover % in four vegetation layers in 1989 and 2021 in sample plots with initial ash (n=27) or elm dominance (n=27), respectively. *P*-values according to GLMM. *P* < 0.05 in bold face.

	Ash dom. 1989			Elm dom. 1989		
	1989	2021	<i>P</i>	1989	2021	<i>P</i>
<i>Mean cover</i>						
Upper tree layer	76	51	<0.001	78	31	<0.001
Lower tree layer	21	26	0.718	30	29	0.940
Shrub layer	27	30	0.567	19	31	0.006
Ground layer	163	144	0.016	162	146	0.041
<i>Species richness</i>						
Upper tree layer	2.9	2.5	0.300	2.5	1.5	0.004
Lower tree layer	2.7	2.7	0.930	1.8	2.1	0.322
Shrub layer	4.8	4.9	0.886	3.4	5.1	<0.001
Ground layer	27.5	24.6	0.009	19.3	20.6	0.162

Species richness decreased in the upper tree layer and increased in the shrub layer, respectively, in plots dominated by elm in 1989. 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, while the cover of species with low shade traits only increased in the shrub layer between 1989 and 2021 (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 of species with low shade traits did not increase in any layer (Table 2).

Table 2. Mean cover % of elm, ash, other high and low shade woody species, respectively. 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 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.

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

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. This indicates that although there were general changes in species composition over time, these differed between ash and elm stands mainly in the case of the tree layers. This was confirmed by the pairwise perMANOVA which 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 ($\Delta 0.26$) than in those that were ash-dominated ($\Delta 0.16$). 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 ($\Delta 0.05$) in the ground layer of the elm-dominated plots, which wasn't the case in the ash-dominated ($P = 0.186$, $\Delta 0.02$).

According to the NMDS analyzes, 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 the centroids of the initially elm-dominated plots were located closer to those of the ash-dominated plots from the second inventory than from 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). While less nutrient-rich plots changed towards a higher share of beech, more nutrient-rich plots changed towards hornbeam (*Carpinus betulus*) or small-leaved lime. Likewise, wetter plots turned towards a higher share of black alder (*Alnus glutinosa*) and bird cherry (Fig. 2, Table A1).

Discussion

Our results show that the 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 to the study region about 20 years earlier than ADB. Elm has almost completely disappeared from the upper tree canopy across all plots studied, and only a few single larger elm individuals remain alive in a small number of plots initially dominated by ash. 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 a number of years before individual stems reach this size (Thomas et al. 2018).

While the large-scale loss of elm from the tree layers in elm-dominated plots has resulted in a clear expansion of other woody species in all layers, the observed expansion in ash-dominated plots was less pronounced. This is probably explained by the more recent disturbance and the smaller cover loss of ash in the tree layers so far. With the persistent advance of ADB, it seems only a matter of time until ash is also lost from the tree canopy in most of our study sites (Ruks 2020, Matisone et al. 2021). However, between 1989 and 2021, DED also provided ash with a brief window of opportunity to fill emerging canopy gaps. For example, in the Swedish forest reserve Dalby Söderskog, ash managed to increase its abundance considerably until the arrival of ADB (Brunet et al. 2014).

Wind-dispersed spores of the fungus causing ADB are infecting trees via leaves and rachises, before colonizing twigs and branches. The resultant disruption of nutrient and water transport leads to the progressive dieback of the shoots, branches and crown, ultimately resulting in the tree's death (Cleary et al., 2013; Hultberg et al., 2020). ADB thus affects trees of all sizes, which explains the loss of ash across the different canopy layers. In contrast to DED which readily kills individual stems within a few years, infected ash trees may temporarily recover and even increase in canopy cover by forming new adventitious shoots. Whereas this may slow down the rate of ash loss, there are no indications that badly damaged trees can make a long-lasting recovery (Thomas 2016, Skovsgaard et al. 2017, Stener 2018, Matisone et al. 2021).

Even without the arrival of DED and ADB, one would expect some degree of successional changes to have occurred during the study period. Although there are no unaffected sites left to demonstrate such non-pathogen induced changes, evidence from the decades prior to the arrival of DED and ADB appears to indicate their potential. Two long-term case studies from southern Sweden and additional analyses of canopy structures in elm- and ash-dominated forests suggest a persistent or even increasing dominance of elm in all canopy layers in the decades prior to 1989 (Malmer et al. 1978, Brunet 1991, Diekmann 1994, 1999, Brunet et al. 2014, Hytteborn et al. 2017). Elm often regenerated under ash canopies while the reverse was much less common. This would have resulted in overall denser and darker forests at the moist eutrophic site conditions studied here.

Confirming our hypothesis, the multivariate 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 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. In this context, it is important to stress that this increase in β -diversity may not increase the diversity on the landscape level to any large extent and thus be of minor importance to conservation of forest biodiversity. At the same time the loss of ash and elm may have severe effects on other taxonomic groups more directly connected to the trees (e.g. epiphytes, invertebrates, Mitchell et al. 2014, 2016, 2017, Thomas et al. 2018, Hultberg et al. 2020).

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 fully compensated for the loss of the previous dominants in the upper canopy. 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 in the understory and availability of seed trees nearby. The speed of this process will be influenced by life-history traits, such as growth patterns, seed production and dispersal, interacting 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).

Within the potential dominance ranges of elm and ash, beech is most competitive in less moist and nutrient rich sites, and has increased in several plots with such conditions. However, many sites are too moist for beech, as well as probably being too moist for Norway maple and small-leaved lime (Diekmann 1994, 1999, Leuschner and Ellenberg 2017). Black alder, and to a lesser extent hornbeam and pedunculate oak, grow on moist soils, but are not always part of the local forest community. When oak is already present in a site, and ungulate browsing pressure is low, natural regeneration of the light-demanding oak can be abundant in large gaps (Brunet et al. 2014). In most areas, however, successful establishment of oak depends on protection from ungulate browsers (Leonardsson et al. 2015, Petersson et al. 2019). Bird cherry and hazel have also increased their cover in several plots, but do not grow tall enough to become part of the upper canopy. These distinctions in the ecology and physiognomy of the local tree species pool imply that some forests are unlikely to recover their previous stand structure in the foreseeable future.

Despite the prevalence of disease-induced canopy gaps in many of our plots, colonization by shade-intolerant early successional tree species such as aspen (*Populus tremula*) and birches (*Betula pendula*, *B. pubescens*) was almost absent (cf. Table A1). This is in contrast to findings from Latvia, 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 Latvia 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 of ash (as the

area was not yet affected by ADB), bird cherry, hazel, Norway maple and young elm, whereas aspen, birch, and pedunculate oak all failed to regenerate despite the prevalence of ample seed sources.

In the mostly 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 (Leuschner and Ellenberg 2017). 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, as did black alder and small-leaved lime on occasion.

Third, existing saplings and advanced regeneration of shade-tolerant trees increase their growth rates (Kern et al. 2017). 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 (cf. 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 was 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, 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.

Declarations

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Competing Interests

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

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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Figures

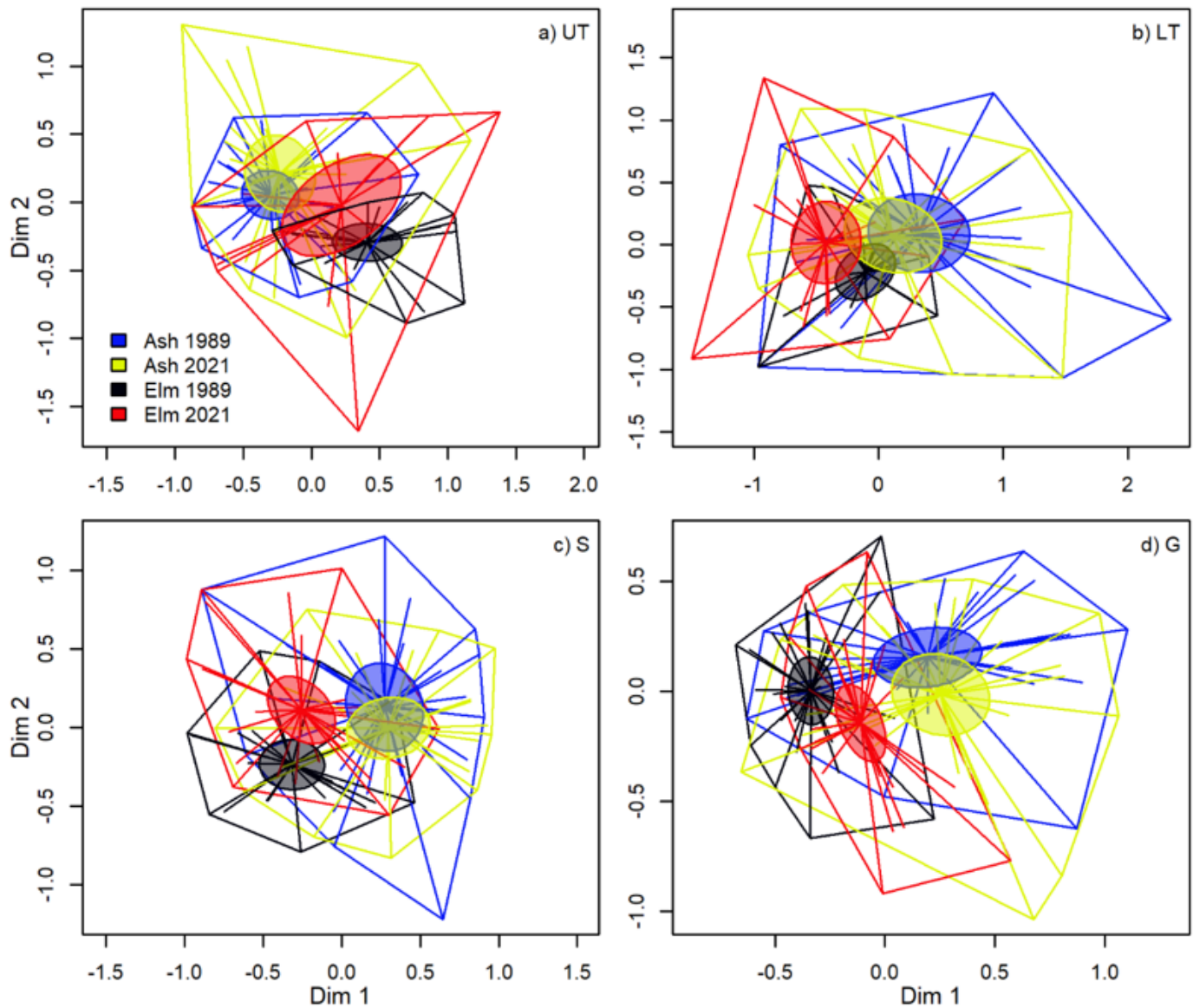


Figure 1

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.

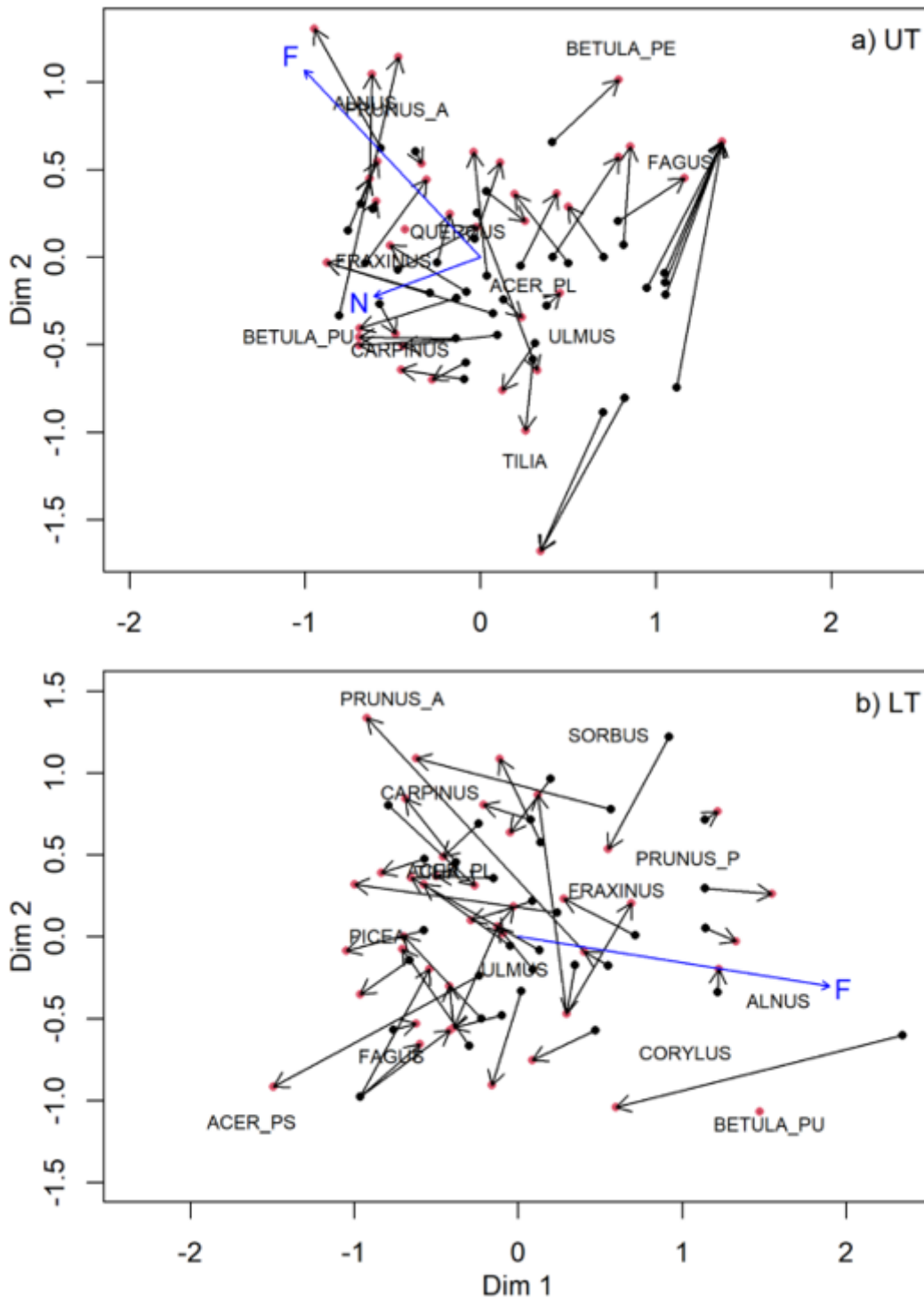


Figure 2

The position of species (see 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).

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