

## Ash dieback: A single-species catastrophe or a cascade of ecological effects in the ground flora?

Fride Høistad Schei<sup>a,\*</sup>, Mie Prik Arnberg<sup>a</sup>, John-Arvid Grytnes<sup>b</sup>, Maren Stien Johanesen<sup>b</sup>, Jørund Johansen<sup>a</sup>, Anna Birgitte Milford<sup>a</sup>, Anders Røyenstrand<sup>c</sup>, Mari Mette Tollefsrud<sup>d</sup>

<sup>a</sup> Norwegian Institute of Bioeconomy Research, Bergen, Norway

<sup>b</sup> Department of Biological Sciences, University of Bergen, Bergen, Norway

<sup>c</sup> Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

<sup>d</sup> Norwegian Institute of Bioeconomy Research, Ås, Norway

### ARTICLE INFO

#### Keywords:

*Hymenoscyphus fraxineus*  
Forest  
*Fraxinus excelsior*  
Ecosystem  
Non-native species  
Pathogen  
Pest

### ABSTRACT

Climate change and human activities have accelerated the spread of non-native species, including forest pests and pathogens, significantly contributing to global biodiversity loss. Pathogens pose a significant threat to forest ecosystems due to a lack of coevolution with native hosts, resulting in ineffective defence mechanisms and severe consequences for the affected tree species. Ash dieback, caused by the fungus *Hymenoscyphus fraxineus*, is a relatively new invasive forest pathogen threatening ash (*Fraxinus excelsior*) with mortality rates in northern Europe reaching up to 80%. The loss of ash due to dieback has severe ecological implications, potentially leading to an extinction cascade as ash provides crucial habitats and resources for many organisms. Despite this, the consequences of ash dieback on associated communities are largely unknown. To address this, we analysed changes in species richness, vegetation structure, and composition in 82 permanent vegetation plots across 23 Norwegian woodlands. We compared data collected before and 10–14 years after the emergence of ash dieback. In these woodlands, ash significantly declined in cover, leading to changes in tree species composition and facilitating the establishment of other woody tree species like hazel (*Corylus avellana*) and the invasive species sycamore (*Acer pseudoplatanus*). Despite these changes in the tree species composition, no significant alterations were observed in the understory plant community, indicating a degree of ecosystem resilience or a lagging community response. At this point, and with our focus on the vascular plants, we do not find support for cascading effects due to ash dieback. However, our findings demonstrate that one invasive species is facilitating the expansion of another, raising concerns about potential ecological imbalance and cascading effects in the future.

### 1. Introduction

Climate change and human activities have significantly accelerated the movement of species into new environments, leading to an increase in the prevalence of non-native species. These species are recognised as one of the five primary drivers of global biodiversity loss (Maxwell et al., 2016; Seebens et al., 2017; IPBES, 2019). Among them, non-native forest pests or pathogens have significantly increased over the past century, leading to new tree diseases worldwide (Freer-Smith and Webber, 2017). These new diseases often have severe consequences for forest ecosystems, as trees lack effective defence mechanisms due to the absence of coevolution (Paap et al., 2022).

Dutch elm disease and chestnut blight are examples of diseases leading to catastrophic pandemics causing a significant decline in tree populations and altered forest composition and structure (Hubbes, 1999; Jacobs, 2007; Potter et al., 2011; Brunet et al., 2014). Similarly, ash dieback, which is caused by the fungus *Hymenoscyphus fraxineus*, is currently threatening the entire population of European ash (*Fraxinus excelsior*, hereafter referred to as ash) (Gross et al., 2014). *H. fraxineus* harms ash by colonizing internal tissues, leading to leaf and stem necrosis, crown dieback, and root collar necrosis, often resulting in tree death (Gross et al., 2014). In contrast, in northeastern Asia where *H. fraxineus* is native, the fungus is harmless to the local ash (*F. manshurica*) (Zhao et al., 2012; Zheng and Zhuang, 2014). Ash

\* Corresponding author.

E-mail address: [fride.schei@nibio.no](mailto:fride.schei@nibio.no) (F.H. Schei).

<https://doi.org/10.1016/j.foreco.2024.122322>

Received 10 July 2024; Received in revised form 30 September 2024; Accepted 1 October 2024

Available online 18 October 2024

0378-1127/© 2024 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

dieback was first reported in Europe, specifically in Poland, in the early 1990s (Przybyl, 2002). Due to its effective long-distance dispersal (Kowalski and Holdenrieder, 2009), the disease is now widespread throughout Europe (Timmermann et al., 2011; McKinney et al., 2014). Northern regions are experiencing high mortality rates of up to 80 %, compared to 20 % in southern Europe, where the disease emerged later and is advancing more slowly (George et al., 2022).

Studies have found that dead ash trees are being replaced by other tree and bush species (Matison et al., 2021; Brunet et al., 2023). This replacement is expected to alter environmental conditions, impacting ecosystem services and associated species (Mitchell et al., 2014, 2016). Ash is a keystone species, particularly in the northern regions of Europe, providing habitats for many species (Hultberg et al., 2020). Mitchell et al. (2014) estimated that in the UK, more than a thousand species are associated with ash, including birds, mammals, invertebrates, fungi, lichens and plants, with 106 either obligate or highly associated with ash. These species rely directly on ash as a habitat or indirectly through the habitat conditions created by ash. Ash creates specific habitat conditions by producing rich and easily decomposable leaf litter (Langenbruch et al., 2012), facilitating high nutrient cycling rates and maintaining high soil pH (Oostra et al., 2006; Jacob et al., 2009). Additionally, the relatively open canopy of ash allows higher light levels to reach the ground compared to other tree species (Emborg, 1998). Therefore, the replacement of ash by other bush or tree species is expected to have significant implications for the understory ecosystem. Grave predictions warn of an extinction cascade affecting species dependent on ash-sustained environments (Hultberg et al., 2020). However, there are no comprehensive field studies, to our knowledge, investigating how ash dieback is affecting understory species communities. Understanding these impacts is essential for predicting the cascading ecological consequences of ash dieback.

Ash reaches its northernmost range in Norway and is one of the most common tree species in Europe's northern broadleaved deciduous forests. However, ash is rarely found in pure stands; instead, it coexists with other tree species such as hazel (*Corylus avellana*), oak (*Quercus* spp.), small-leaved lime (*Tilia cordata*), and wych elm (*Ulmus glabra*). Together, these broadleaved species constitute less than 1 % of Norway's total forest cover, yet they are notable for their high species richness and biodiversity value, supporting 30 % of the forest-associated red-listed species in Norway (Norwegian biodiversity information centre, 2021).

Ash dieback was first observed in Norway in 2008 (Talgø et al., 2009). Since then, it has spread throughout the distribution range of ash in Norway, causing a dramatic population decline (Timmermann et al., 2017). This decline has resulted in the categorisation of ash as "vulnerable" on the Norwegian red-list (Solstad et al., 2021). At the western coast of Norway, ash dieback is currently the only pathogen registered in the broadleaved deciduous woodlands (Timmermann et al., 2023).

To assess the impact of ash dieback on species-richness, vegetation structure and composition, we utilised a network of 82 permanent plots within 23 mixed-species woodlands in Norway. Here, we compare vegetation surveys of vascular plants conducted prior to the emergence of ash dieback with resurveys conducted 10 to 14 years after the emergence of ash dieback. The objective was to determine whether ash dieback has led to a solitary-species catastrophe or if it has triggered a series of ecological cascades within the understory plant community. Specifically, we hypothesize (H1): The decrease in the cover of ash trees has been more pronounced compared to other tree species; (H2): Plots affected by ash dieback have exhibited notable alterations in their understory plant community; (H3): Plots affected by ash dieback have shifted their understory plant community towards a composition of more light demanding species.

## 2. Materials and methods

### 2.1. Study area

The study area is located on the western coast of Norway (Fig. 1) and is part of the most northern broadleaved deciduous forest in Europe, situated in a climatic transitional zone between the nemoral deciduous forests to the south and the extensive boreal coniferous forest to the north. The 23 study sites (Fig. 1), which includes both forest reserves and non-reserve areas, show no evidence of recent management. Signs of historical forest management are limited to old individual trees, many of which are centuries-old pollards. All the woodlands studied are old-growth, semi-natural broadleaved forests, ranging from over 140–200 years in age (Norwegian forest resources map; Astrup et al., 2019). Stem density across these forest stands varies between 1100 and 2000 trees per hectare, with differences both within and between sites (Norwegian forest resources map; Astrup et al., 2019). Ash is present at all sites, but tree species composition varies particularly due to the clear west-east climatic gradient in the study area, ranging from an oceanic climate along the coast and in the outer parts of the fjord district, to a weakly continental climate at the heads of the fjords.

### 2.2. Vegetation surveys

Our study utilised vegetation plots of vascular plants originally intended for long-term research on anthropogenic changes, like global warming and lack of traditional management. Collected between 2007 and 2009, this data now serves as a valuable baseline for our research, as it was gathered just a few years before the onset of ash dieback in the study region. Study A, led by Fride H. Schei, followed a sampling protocol akin to a set of quasi-permanent vegetation plots from 1979, employing cover estimations after Hult-Sernander scale (Du Rietz, 1921), and a fixed plot size of 25 m<sup>2</sup>. During the field work in 2007–2009 all plots were marked with metal stakes for future resurveying. Study B, led by Anders Rønstrand, used previously established permanent plots documented by Moe (1995), with size ranging from 9 to 60 m<sup>2</sup>. The field work was conducted in 2008–2009, all plots were marked with red paint on rocks, rock walls or sticks.

Between 2018 and 2022, 82 of the permanent plots surveyed between 2007 and 2009 were resurveyed. The resurveyed plots comprised 62 plots from Study A and 20 plots from Study B. To minimize potential bias: i) each plots was resurveyed within  $\pm 10$  days of the original survey to account for seasonal variation, ii) only plots with intact permanent marks were included to reduce relocation errors, iii) all field surveyors were thoroughly trained prior to conducting the surveys. The plots are strategically located across 23 broadleaved deciduous woodlands, with 42 plots in nature reserves and 40 in non-protected woodlands (Fig. 1). The resurveys took place between 10 and 14 years after the original survey and 7–11 years after the arrival of ash dieback.

The plot size and sampling methodology remained consistent between the original surveys and the resurveys. In each plot, vascular plants were stratified into three vegetation layers: the field layer (< 0.5 m), the bush layer (0.5–2 m), and the tree layer (> 2 m), bush and tree layer combined referred to as overstory, and field layer is referred to as understory. Tree and bush species appearing in the field layer are categorised as seedlings or juveniles. Species covers within these layers were estimated using a five-graded scale defined for estimating plant cover, after Hult-Sernander scale (Du Rietz, 1921), referred to as Variant A (Pätsch et al., 2019), with standardized cover categories: 1 = >0–6.25 %, 2 = 6.25–12.5 %, 3 = 12.5–25 %, 4 = 25–50 %, and 5 = 50–100 %. Certain species were grouped: *Dryopteris filix-mas* and *Dryopteris affinis*, *Polystichum aculeatum* and *Polystichum braunii*, and *Ranunculus acris* and *R. auricomus*.agg.

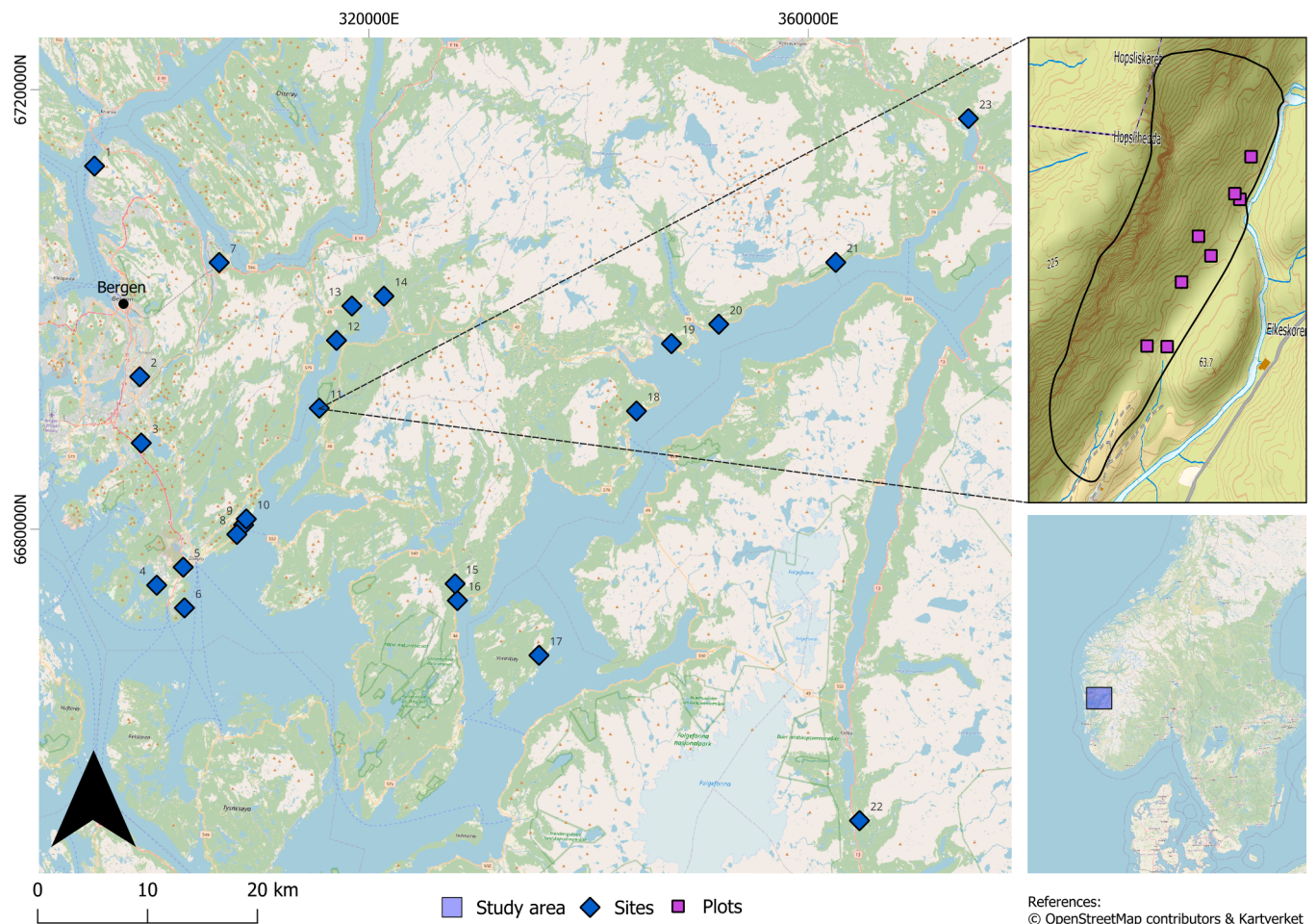


Fig. 1. Map of the study area with the 23 study sites marked by blue diamonds. Upper right: Close-up of study site 11, displaying the distribution of its 8 study plots by purple squares. Lower right: Blue square displaying the location of the study area on the western coast of Norway.

### 2.3. Assessment of ash dieback

Key symptoms of ash dieback include crown defoliation, dead twigs, and tree mortality, all of which result in significant changes in the canopy cover (Timmermann et al., 2017), and monitoring these canopy changes is essential for tracking the progression of the disease. The visual assessment of crown damage is the most common method for detecting ash dieback and is also used by ICP Forests Level 1 forest damage survey to evaluate its impact (George et al., 2022).

### 2.4. Statistical analysis

We transformed the cover classes into the percentage species cover using the mean of each cover class following Pätzsch et al. (2019): 0 = 0 %, 1 = 3.63 %, 2 = 9.38 %, 3 = 18.78 %, 4 = 37.50 %, 5 = 75 %. We considered plots to be affected by ash dieback when ash cover in the tree layer decreased from class 3, 4 or 5 (> 18 % ash cover) to class 0, 1 or 2 (0–9 % ash cover) between sampling periods. That is, when the ash cover decreased from ‘high’ to ‘low’ or ‘high’ to ‘no’ cover in the tree layer, a plot was considered to be affected by ash dieback. All statistical analyses were conducted in R version 4.3.2 (R Core Team, 2023).

To evaluate changes in percentage cover of individual species between the two sampling periods, we used non-parametric Wilcoxon signed-rank tests for paired samples across the three vegetation layers (tree, bush, and field layer). Species that were registered in fewer than 25 plots, combining both the initial survey and the resurvey, in a vegetation layer were excluded from the respective layer analysis and *p*-values were adjusted with a Benjamini–Hochberg false discovery rate

(FDR) correction (Benjamini and Hochberg, 1995) for multiple comparisons (alpha level = 0.05).

We examined the decreased shading capacity of overstory layers as changes in the total cover of tree and bush species, and the combined cover of overstory layers using generalized linear mixed models (GLMMs, ‘glmmTMB’ function from glmmTMB package; Brooks et al., 2017). Tree and bush cover were calculated as the cumulative cover of species within plots in their respective layers while the total overstory cover was calculated as the cumulative cover of tree and bush species. This approach allowed us to assess shading effects, where an increase in the bush layer potentially could mask the loss of tree layer cover or where a decrease in the bush layer could further reduce overstory shading. The three models included the explanatory variables ‘ash dieback’ (yes/no), ‘sampling period’ (old/new) and their interaction as fixed effects. Plot ID nested within site were included as a random factor to account for spatial proximity of plots within sites and repeated sampling of plots. Different distributions were used based on the response variable and model fit: Gaussian distribution for tree cover and total overstory cover and a Tweedie distribution for the bush cover to account for large number of zeroes. We evaluated the marginal significance of predictor variables with a Type II Wald chi-square test (‘Anova’ function in the car package; Fox and Weisberg, 2019). For significant interactions, we applied a pairwise contrast between sampling periods within each level of ash die-off impacted with a Tukey’s post hoc test (‘emmeans’ function in the emmeans package; Lenth, 2024). For all models, we confirmed that model assumptions were met by checking for distribution of residuals, homogeneity of variance, independence, and overdispersion where applicable.

To evaluate the impact of ash dieback on understory vegetation, we employed GLMMs with explanatory and random variables, marginal significance and contrast testing as detailed above. Our response variables included species richness, diversity and total cover and cover-weighted mean (cwm) Ellenberg species indicator values for light (Ellenberg et al., 1992) for each plot. Species diversity was calculated as the Shannon's diversity index with the 'diversity' function from vegan package (Oksanen et al., 2022). The models were fitted with a zero-truncated Conway–Maxwell–Poisson distribution for species richness to handle underdispersion and lack of zeros and Gaussian distributions for species diversity, cover and cwm Ellenberg light values. Furthermore, we assessed compositional shifts in field layer vegetation across sampling periods, ash dieback status (affected/unaffected) and their interaction using a permutational multivariate analysis of variance (PERMANOVA) with the 'adonis2' function in the vegan package (Oksanen et al., 2022). Given the significant interaction, we applied pairwise PERMANOVAs to test differences in composition between sampling periods within the levels of ash dieback status. All PERMANOVA tests were implemented with 999 permutations and Bray–Curtis dissimilarity matrices and permutations restricted to 'plot ID' to accommodate the paired sample design. To account for multiple comparisons, *p*-values were adjusted with the FDR correction. As PERMANOVA can be sensitive to differences in multivariate dispersions (Anderson and Walsh, 2013), we subsequently performed an analysis of multivariate homogeneity (PERMDISP; Anderson et al., 2006) and pairwise comparisons using the 'betadisper' and 'permutest' functions with Bray–Curtis distances in the vegan package. Changes in species composition were visualized using a non-metric multidimensional scaling (NMDS) ordination with three axes on bray Curtis-distances (stress = 0.18) using the metaMDS function in the vegan package (Oksanen et al., 2022).

### 3. Results

Across the three vegetation layers, a total of 156 species were consistently observed in both the original vegetation survey and the subsequent resurvey. Specifically, 18 species were identified in the tree layer, 18 in the bush layer, and 150 in the field layer. Within the field layer, eight species were seedlings or juvenile bush and tree species, while 142 were herbaceous plants or dwarf shrubs. In the first sampling period (i.e. original survey) ash was detected in the tree layer in 58 out of 82 plots, and in 52 plots during the second sampling period. Of the initial 58 plots with ash, 25 had high ash cover (cover > 18 %) in the first sampling period, and of those, 21 plots had decreased to low ash cover (cover < 9 %) by the second sampling period. Meanwhile, the cover of ash had increased from low to high in five plots, and in total, in the second sampling, 12 plots had high ash cover while 40 plots had low ash cover.

Among the six species with sufficient sample size in the tree layer, ash was the only species that showed a decrease in tree cover from the first sampling period (mean: 15.77 %) to the second sampling period (6.44 %;  $p = 0.001$ ; Table 1; Fig. 2). In contrast, the mean cover of sycamore (*Acer pseudoplatanus*), increased from 2.32 % to 5.06 % ( $p = 0.011$ ; Table 1; Fig. 2). The other four tree species, wych elm, hazel, bird cherry (*Prunus padus*) and small-leaved lime, did not show a significant change in cover between the sampling periods (for all,  $p > 0.05$ ; Table 1; Fig. 2; Figure S1). In the bush layer, ash was the only species to decrease in mean cover between the first and second sampling period ( $p = 0.031$ ), while hazel showed the highest cover increase followed by sycamore ( $p = 0.014$  and  $p = 0.003$  respectively; Table 1; Fig. 2; Figure S1). Cover of bird cherry and wych elm remained stable ( $p > 0.05$ ; Table 1; Fig. 2). In the field layer, ash did not show cover change, i.e. the cover of ash seedlings and juveniles remained constant between sampling periods ( $p = 0.861$ ; Table S1). Notably, the percentage cover of sycamore seedlings nearly doubled, from 0.82 % to 1.9 %, between sampling periods ( $p = 0.036$ ; Table S1). Among the 46 herbaceous species with sufficient

**Table 1**

Results of the paired Wilcoxon signed rank test and mean cover of species in the tree and bush layer between the first and second sampling period. Only species that occurred in minimum 25 of the paired plots where tested. Significant *p*-values are marked in bold.

Layer	Species	Sampling period		<i>p</i> -value
		First Mean ± SE	Second Mean ± SE	
Tree	Sycamore	2.32 ± 1.12	5.06 ± 1.77	<b>0.011</b>
	Hazel	10.86 ± 2.52	10.53 ± 2.38	1
	Ash	15.77 ± 2.18	6.44 ± 1.09	<b>&lt; 0.001</b>
	Bird cherry	2.85 ± 1.27	2.53 ± 0.96	0.908
	Small-leaved lime	11.35 ± 2.72	12.36 ± 2.81	0.541
	Wych elm	27.39 ± 3.38	25.19 ± 3.36	0.332
Bush	Sycamore	0.74 ± 0.26	1.75 ± 0.56	<b>0.014</b>
	Hazel	6.68 ± 1.91	11.08 ± 2.41	<b>0.003</b>
	Ash	2.91 ± 0.67	1.08 ± 0.22	<b>0.031</b>
	Bird cherry	0.77 ± 0.21	0.80 ± 0.25	0.882
	Wych elm	0.63 ± 0.18	0.84 ± 0.26	0.183

sample size, four species experienced an increase in cover, while three decreased between sampling periods (Table S1).

In plots with decreasing ash cover, presumably due to ash dieback, the average tree cover declined by 23 % between sampling periods ( $t = -4.122$ ,  $p < 0.001$ ) while the average bush cover increased by 8.39 % ( $t = 4.70$ ,  $p < 0.001$ ; Fig. 3a and b; Table S2). Conversely, in plots unaffected by ash dieback, where there was no change or absence of ash cover, tree cover remained stable with a negligible decrease of  $-0.48$  % between sampling periods ( $t = -0.156$ ,  $p = 0.876$ ), and bush cover exhibited a modest increase of 2.08 % ( $t = 2.187$ ,  $p = 0.070$ ). Further, the interaction between sampling period and ash dieback status did not significantly impact the overall cover of the overstory layer, which combined both tree and bush layer ( $\chi^2 = 2.760$ ,  $p = 0.097$ ; Table S2; Fig. 3c).

In the field layer, species richness, diversity and cover were unaffected between sampling periods ( $p > 0.05$  for all; Fig. 4; Table S2). In general, plots affected by the ash dieback had a slightly higher species diversity; the mean diversity in plots affected by the ash dieback was  $2.65 \pm 0.48$  compared to  $2.38 \pm 0.66$  in unaffected plots (Fig. 4b). The species composition of vascular plants was significantly associated with sampling period, ash dieback and their interaction (Table S3), although the total contribution of the variables was small ( $R^2 = 0.03$ ). Species composition changed between sampling periods both in plots unaffected and affected by the ash dieback ( $p < 0.05$ , Table S3). However, the compositional shift, although significant, was only minor and explained very little of the variation of the data ( $R^2 = 0.005$  and  $R^2 = 0.024$ ; Table S3; Figure S2). Differences in species composition between sampling periods were not driven by dispersion within groups (distance to centroid) in either the unaffected plots (PERMDISP:  $F_{(1,112)} = 0.585$ ,  $p = 0.422$ ) or the affected plots ( $F_{(1,48)} = 0.133$ ,  $p = 0.716$ ). Lastly, plots affected by ash dieback did not move towards a more light-demanding understory community (Table S2; Fig. 4d). In the first sampling, the mean cwm Ellenberg light value for plots affected by the ash dieback was  $2.97 \pm 0.57$  compared  $2.92 \pm 0.521$  in the second sampling.

## 4. Discussion

### 4.1. Decline of ash and shifts in tree species composition

Our research identified a substantial decline in the abundance of ash over the past decade, resulting in a shift in tree species composition within woodland plots where ash previously thrived. In contrast, plots that initially had little, or no ash cover maintained a relatively stable tree species composition over our study period of 10–14 years. Tree cover loss can result from various stress factors, such as drought, temperature fluctuation, wind, and diseases (Bussotti et al., 2024). However, our finding that ash was the only species in mixed-species forest stands to experience severe decline strongly supports that the

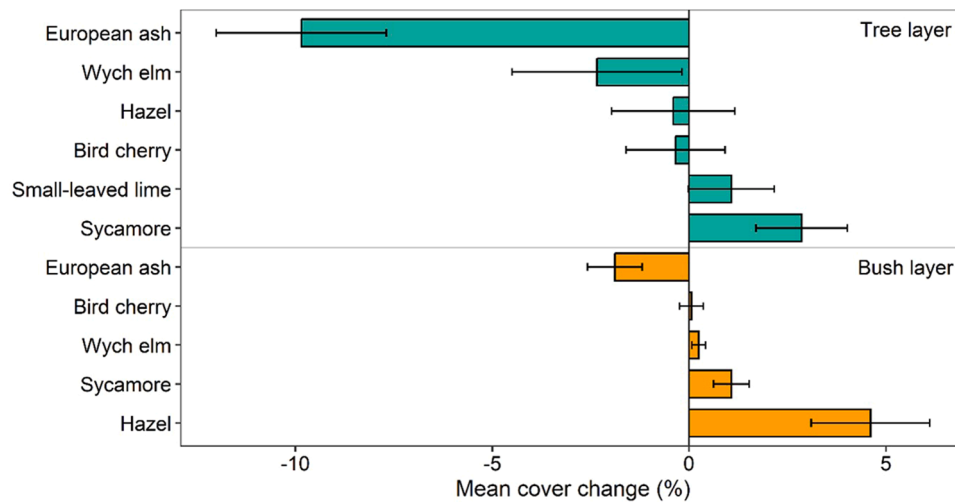


Fig. 2. Mean cover change of species in the tree layer and bush layer in plots between the first and second sampling period. Error bars indicate standard error and asterisk denotes significant changes. Only species that occurred in minimum 25 of the paired plots where tested.

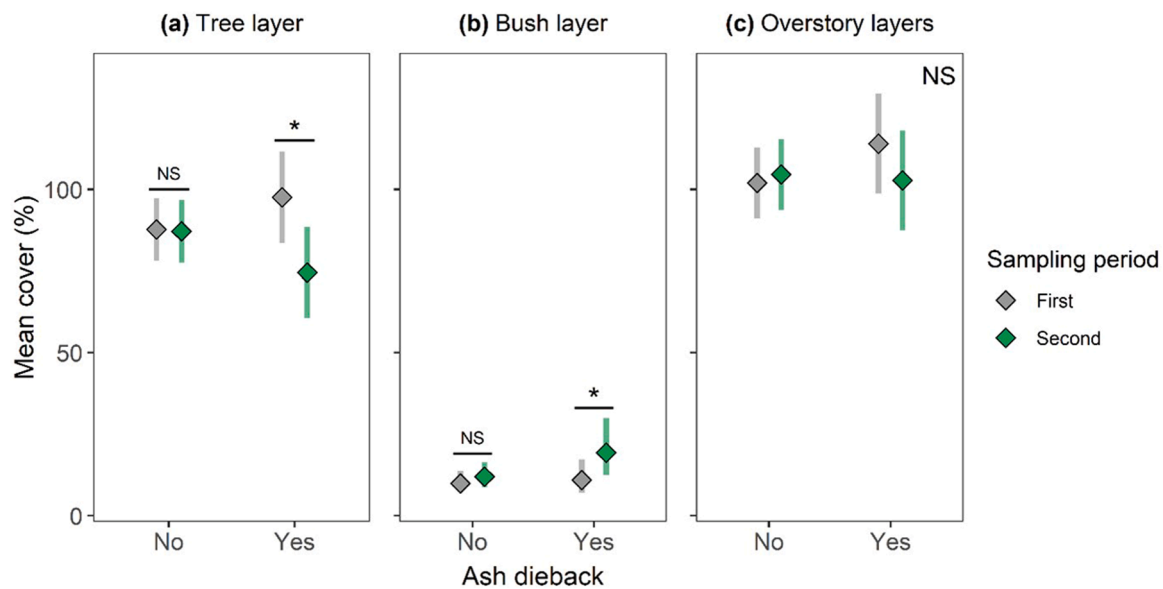


Fig. 3. Differences in mean cover of the a) tree layer, b) bush layer and c) overstory layers (tree and bush layers combined) between sampling periods in plots affected and unaffected by ash dieback. Large points and error bars represent model estimated means and their corresponding 95 % confidence interval. Asterisks indicates significant difference between means within levels ash dieback after a post-hoc Tukey test.

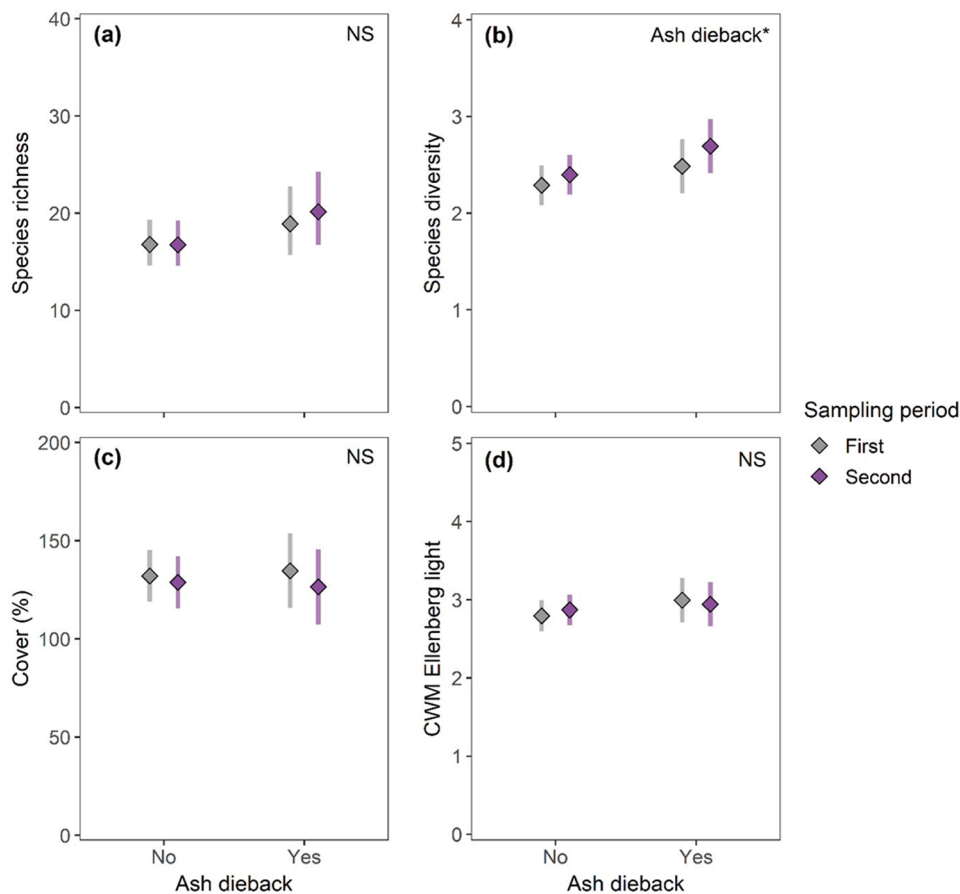
genus-specific pathogen *Hymenoscyphus fraxineus* causing ash dieback, is currently the primary driver of compositional changes in tree species within the northern range-margin populations of European deciduous temperate woodlands. This aligns with results from Norwegian forest monitoring plots, which report a high mortality rate of ash trees, with a staggering 87 % of the trees showing symptoms of dieback (Timmermann et al., 2023).

In our study, the decline of ash has led to canopy openings, facilitating the establishment and expansion of the native species hazel in the bush layer and the non-native species sycamore in the tree, bush, and field layers. We infer that these changes in woodland ecosystems are predominantly in their initial phase, marked by existing trees expanding their crowns to fill the gaps left by sick or dying ash trees. This phase is characterized by the rapid growth and crown expansion of neighbouring trees, which take advantage of the newly available light and space (Matisone et al., 2021). Both hazel and sycamore are predicted to be able to rapidly occupy gaps left by declining ash (see Kirby et al., 2014; Needham et al., 2016; Broome et al., 2019; Evans, 2019). The increase in

hazel aligns with the results from Matisone et al. (2021), who observed the formation of dense shrubland of hazel and wild cherry (*Prunus avium*) in previously ash-dominated forest stands. Hazel is recognized as a stress-competitor (Grime, 2006), and is assumed to benefit from recent canopy openings, at least in the short term (Kirby et al., 2014).

Sycamore has increased its cover in all vegetation layers, with particular concerns related to the doubling of seedlings and juveniles. This highlights sycamore's competitive advantage and potential to fill the ecological niche left by the declining ash. Sycamore is classified as a severe ecological threat on the Norwegian alien species list (Hegre et al., 2023). The ecological consequences of a sycamore invasion are not yet known, but given its competitive traits and longevity, we expect long-term ecological shifts that could significantly affect future dynamics, species composition, and overall forest structure. This situation exemplifies how one invasive species can facilitate the expansion of another, potentially leading to further ecological imbalance.

In the longer term, the replacement of ash by other tree species is expected to induce changes in nutrient cycling, carbon storage, and soil



**Fig. 4.** Estimated means of a) species richness, b) species diversity, c) percentage cover and d) community weighted Ellenberg light values of the field layer vegetation between sampling periods. The interaction between sampling period and ash dieback was not significant in any of the models ( $p > 0.05$  for all, see Table S3). Large points and error bars represent model estimated means and their 95 % confidence interval.

formation, ultimately reshaping ecosystem function and triggering cascading effects on associated communities (Mitchell et al., 2014; Hultberg et al., 2020). Our forest system comprises mixed deciduous stands where ash is one of several tree species. In heterogeneous forest stands, environmental variables such as pH, soil moisture, and nitrogen availability arise from interactions between closely situated tree species, for example, through litter mixing or canopy shading (Ball et al., 2008; Barbier et al., 2008). Since ash rarely dominated the forest stands within our study area but was part of a diverse canopy structure, it may be functionally redundant in terms of regulating nutrient or shading regimes (Mori et al., 2017). Therefore, when ash is reduced or lost, other tree species can compensate, indicating a degree of ecosystem resilience to ash dieback (Hill et al., 2019). For example, the increased cover of hazel and sycamore has swiftly mitigated elevated light transmittance to the ground vegetation, which is an important driver of species composition and diversity in forests (Wulf and Naaf, 2009). Additionally, sycamore has been identified as functionally similar to ash (Mitchell et al., 2016), and both hazel and sycamore are presumed to offer suitable alternative habitats and conditions for many ash-associated species (Mitchell et al., 2014), which might explain the lack of changes in the ground flora.

#### 4.2. Temporal lag or resistance in understory species composition

The lack of consistent change in the understory ground flora might be due to a temporal lag in the community response, as changes in light and microclimatic conditions may occur too rapidly for the ground flora to keep pace. Temporal lag in ground vegetation response has been observed in several forest communities (Bertrand et al., 2011;

Pacheco-Riaño et al., 2023). Moreover, these woodlands have a long tradition of management practices influencing light, nutrient, and microclimatic conditions. Historically, these woodlands were managed to meet the demands for firewood, construction timber, and fodder through practices such as pollarding, coppicing, and grazing by domestic animals (Hauge et al., 2014; Milford et al., 2024). These traditional management practices ceased after WWII, and the formerly open woodland pastures have gradually transformed into tall closed-canopy forests, with traces of earlier management reflected only in the shapes of old individual trees. However, these historical practices caused large fluctuations in microclimate, light, and nutrient conditions, and the ground vegetation might be well-adapted to cope with such fluctuations over time.

#### 4.3. Emerging threats

Ash dieback is currently the only tree pathogen causing severe damage to any of the tree species found in our study areas (Timmermann et al., 2023), even though these woodlands consist of mixed deciduous tree species. However, with increased time and rising temperatures, new pathogens such as the emerald ash borer, Dutch elm disease, and oak wilt could emerge. The introduction of pathogens like the emerald ash borer, which has devastated the ash populations in North America (Poland and McCullough, 2006), could potentially destroy the remaining ash population.

The greatest concern, however, is Dutch elm disease. Brunet et al. (2023) report that Dutch elm disease has caused higher mortality rates in Swedish forests than ash dieback. Wych elm, currently the tree species with the highest tree cover in our study plots, has shown a slight, though

not statistically significant decrease over time. Dutch elm disease has not yet been detected within our study area, however, it is spreading in Norway (Timmermann et al., 2023). The arrival of Dutch elm disease in these woodlands is expected to further alter tree species composition and cause substantial disruptions in ecosystem functions and biodiversity. The potential impact of the combination of ash dieback and Dutch elm disease could be particularly severe, as there are many species associated with both ash and wych elm, using one as an alternative host for the other (Hultberg et al., 2020). This suggests that the loss of wych elm compounds the ecological consequences of ash dieback, further destabilising these woodlands and amplifying the threats to species dependent on these two key tree species.

#### 4.4. Recovery of ash populations

Despite a dramatic decline in the ash cover, ash trees continue to persist within our study plots. Large, mature trees can survive for several years after the initial infection of ash dieback due to their larger crown and extensive foliage (Timmermann et al., 2011, 2017). However, this resilience may also indicate the presence of genetic resistance within the population. Genetic resistance within the population is crucial, with European trials estimating that only 1–5 % of ashes are resistant to ash dieback (Pliura et al., 2011; Kjær et al., 2012; McKinney et al., 2014). The heritability of disease tolerance is estimated to be around 0.4, meaning that 40 % of the variation in tolerance can be explained by genetic factors (e.g. Pliura et al., 2011; Kjær et al., 2012). Positively, ash dieback seems to reduce the reproductive success of diseased trees, allowing healthier trees to contribute more to regeneration, thus leading to a more resistant next generation (Semizer-Cuming et al., 2021).

We observed that the number of ash seedlings and juveniles in the ground layer has remained stable. This is particularly notable given that ash dieback often leads to the death of young trees within just a few years of infection, since a single necrosis on the stem may lead to dieback of the top or even the whole tree (Timmermann et al., 2011, 2017). However, the successful growth of ash seedlings and juveniles into healthy adults depends on the combination of genetic, abiotic, and biotic factors and their interactions. If these juveniles grow into healthy adults, their tolerance should endure (Liziniewicz et al., 2022). Therefore, allowing ash dieback to “run its course” without human intervention aligns with the concept of natural selection, favouring trees with high disease tolerance (Skovsgaard et al., 2017). Our finding of the survival of large trees and the constant stable cover of ash seedlings in the ground layer offer a glimmer of hope for the potential recovery of the ash population within our study area.

#### 4.5. Bias and errors related to long-term study

Plot-based long-term vegetation studies are commonly used to assess vegetation trends, but resurveys face challenges such as relocation error, observer bias, seasonal variation, and limitations of the original data (Kapfer et al., 2017; Morrison, 2021; Verheyen et al., 2018). In our study, permanently marked plots reduce relocation error, though slight discrepancies in boundary repositioning between the corners may have affected sampled areas and species. Observer bias can lead to over-looking, misidentification, or misestimation of species (Morrison, 2021). To decrease the observer bias all samplers were familiar with the local flora and received training under close supervision. Timing differences in resampling can also introduce inaccuracies, but our resurveys were conducted within  $\pm 10$  days of the original survey date for each plot. The observed changes in our study were primarily found in tree species, tree species are easy to detect and show minimal seasonal variation.

## 5. Conclusion

Our study identified a substantial decline in ash abundance over the past decade, leading to significant shifts in tree species composition

within affected woodland plots. This decline facilitated the establishment and expansion of hazel and sycamore, with sycamore raising concerns about future ecological imbalances. Despite this, the persistence of ash seedlings offers hope for potential recovery, depending on future disease dynamics and environmental conditions.

At this point and with our focus on vascular plants, we do not find support for cascading effects caused by ash dieback, but there is a need for studies including other organism groups, as well as further long-term ecological studies, as the future of these ecosystems will likely see continued changes in species composition and forest structure. The resilience of ash seedlings and the adaptive response of the ecosystem to new dominant species will be critical in shaping these forests' long-term dynamics and biodiversity. Follow-up studies are essential to deepen our understanding of the long-term consequences and to guide future conservation and management efforts more effectively.

## Funding information

This study was supported by project "Application of traditional knowledge to halt biodiversity loss in woodlands" (TO01000132) financed by the Technology Agency of the Czech Republic and Norway Grants 2014–2021, and by the NIBIO research group Edelframtid at the Norwegian Institute of Bioeconomy Research.

## CRediT authorship contribution statement

**Fride Høistad Schei:** Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Mie Prik Arnborg:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **John-Arvid Grytnes:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Maren Stien Johansen:** Writing – review & editing, Investigation. **Jørund Johansen:** Writing – review & editing. **Anna Birgitte Milford:** Writing – review & editing. **Anders Røynstrand:** Writing – review & editing, Investigation. **Mari Mette Tollefsrud:** Writing – review & editing, Writing – original draft, Conceptualization.

## Declaration of Competing Interest

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

## Data Availability

Data will be made available on request.

## Acknowledgments

The authors thanks Bjørn Moe for providing access to old permanent plots, Magne Sætersdal for field sampling, Rob Lewis for field assistance, and Jutta Kapfer for pre-analysis and insightful discussions.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.122322](https://doi.org/10.1016/j.foreco.2024.122322).

## References

- Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecol. Monogr.* 83, 557–574. <https://doi.org/10.1890/12-2010.1>.
- Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* 9, 683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>.

- Astrup, R., Rahlf, J., Bjørkelo, K., Debella-Gilo, M., Gjertsen, A.-K., Breidenbach, J., 2019. Forest information at multiple scales: development, evaluation and application of the norwegian forest resources map SR16. *Scand. J. For. Res.* 34, 484–496. <https://doi.org/10.1080/02827581.2019.1588989>.
- Ball, B.A., Hunter, M.D., Kominoski, J.S., Swan, C.M., Bradford, M.A., 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. *J. Ecol.* 96, 303–313. <https://doi.org/10.1111/j.1365-2745.2007.01346.x>.
- Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved - a critical review for temperate and boreal forests. *For. Ecol. Manag.* 254, 1–15. <https://doi.org/10.1016/j.foreco.2007.09.038>.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B-Stat. Methodol.* 57, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., Gégout, J.-C., 2011. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479, 517–520. <https://doi.org/10.1038/nature10548>.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400. <https://doi.org/10.32614/rj-2017-066>.
- Broome, A., Ray, D., Mitchell, R., Harmer, R., 2019. Responding to ash dieback (*Hymenoscyphus fraxineus*) in the UK: woodland composition and replacement tree species. *Forestry* 92, 108–119. <https://doi.org/10.1093/forestry/cpy040>.
- Brunet, J., Bukina, Y., Hedwall, P.O., Holmström, E., von Oheimb, G., 2014. Pathogen induced disturbance and succession in temperate forests: Evidence from a 100-year data set in southern Sweden. *Basic Appl. Ecol.* 15, 114–121. <https://doi.org/10.1016/j.baec.2014.02.002>.
- Brunet, J., Felton, A., Hedwall, P.-O., 2023. Vegetation responses to pathogen-induced tree loss: Swedish elm and ash forests revisited after 32 years. *Plant Ecol.* 224, 875–884. <https://doi.org/10.1007/s11258-023-01342-0>.
- Bussotti, F., Potocić, N., Timmermann, V., Lehmann, M.M., Pollastrini, M., 2024. Tree crown defoliation in forest monitoring: concepts, findings, and new perspectives for a physiological approach in the face of climate change. *Forestry* 97, 194–212. <https://doi.org/10.1093/forestry/cpad066>.
- R. Core Team, 2023. R: A Language and Environment for Statistical Computing. In: R Foundation for Statistical Computing, Vienna, Austria.
- Du Rietz, G.E., 1921. The fundamental units of vegetation. *Proc. Int. Congr. Plant Sci.* 1, 623–627.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte von pflanzen in Mitteleuropa. E. Goltze.
- Emborg, J., 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manag.* 106, 83–95. [https://doi.org/10.1016/s0378-1127\(97\)00299-5](https://doi.org/10.1016/s0378-1127(97)00299-5).
- Evans, M.R., 2019. Will natural resistance result in populations of ash trees remaining in British woodlands after a century of ash dieback disease? *R. Soc. Open Sci.* 6. <https://doi.org/10.1098/rsos.190908>.
- Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression. Sage, Thousand Oaks CA.
- Freer-Smith, P.H., Webber, J.F., 2017. Tree pests and diseases: the threat to biodiversity and the delivery of ecosystem services. *Biodivers. Conserv.* 26, 3167–3181. <https://doi.org/10.1007/s10531-015-1019-0>.
- George, J.P., Sanders, T.G.M., Timmermann, V., Potocić, N., Lang, M., 2022. European-wide forest monitoring substantiate the necessity for a joint conservation strategy to rescue European ash species (*Fraxinus* spp.). *Sci. Rep.* 12. <https://doi.org/10.1038/s41598-022-08825-6>.
- Grime, J.P., 2006. Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons, Chichester, UK.
- Gross, A., Holdenrieder, O., Pautasso, M., Queloz, V., Sieber, T.N., 2014. *Hymenoscyphus pseudoalbidus*, the causal agent of European ash dieback. *Mol. Plant Pathol.* 15, 5–21. <https://doi.org/10.1111/mp.12073>.
- Hauge, L., Kvamme, M., Austad, I., 2014. Lauvtrærnes innvandringshistorie og bruken av dem. In: Austad, I., Hauge, L. (Eds.), *Trær og tradisjon: Bruk av lauvtrær i kulturlandskapet*. Fagbokforlaget, Bergen.
- Hegre, H., Solstad, H., Alm, T., Fløistad, I.S., Pedersen, O., Schei, F.H., Vandvik, V., Vøllering, J., Westergaard, K.B., Skarpaas, O., 2023. Magnoliophyta: Vurdering av platanlønn *Acer pseudoplatanus* for Fastlands-Norge med havområder. In: *Artsdatabanken (Ed.), Fremmedartslista*, p. 2023.
- Hill, L., Hemery, G., Hector, A., Brown, N., 2019. Maintaining ecosystem properties after loss of ash in Great Britain. *J. Appl. Ecol.* 56, 282–293. <https://doi.org/10.1111/1365-2664.13255>.
- Hubbes, T., 1999. The American elm and Dutch elm disease. *For. Chron.* 75, 265–273.
- Hultberg, T., Sandström, J., Felton, A., Öhman, K., Rönnerberg, J., Witzell, J., Cleary, M., 2020. Ash dieback risks an extinction cascade. *Biol. Conserv.* 244, 108516. <https://doi.org/10.1016/j.biocon.2020.108516>.
- IPBES, 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. In: Brondizio, E.S., Díaz, J.S., S., Ngo, H.T. (Eds.), *IPBES Secretariat (Ed.)*. Bonn, Germany, p. 1148. <https://doi.org/10.5281/zenodo.3831673>.
- Jacob, M., Weland, N., Platner, C., Schaefer, M., Leuschner, C., Thomas, F.M., 2009. Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. *Soil Biol. Biochem.* 41, 2122–2130. <https://doi.org/10.1016/j.soilbio.2009.07.024>.
- Jacobs, D.F., 2007. Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. *Biol. Conserv.* 137, 497–506. <https://doi.org/10.1016/j.biocon.2007.03.013>.
- Kapfer, J., Hédl, R., Juraskinski, G., Kopecky, M., Schei, F.H., Grytnes, J.A., 2017. Resurveying historical vegetation data-opportunities and challenges. *Appl. Veg. Sci.* 20, 164–171. <https://doi.org/10.1111/avsc.12269>.
- Kirby, K.J., Bazely, D.R., Goldberg, E.A., Hall, J.E., Isted, R., Perry, S.C., Thomas, R.C., 2014. Changes in the tree and shrub layer of Wytham Woods (Southern England) 1974–2012: local and national trends compared. *Forestry* 87, 663–673. <https://doi.org/10.1093/forestry/cpu026>.
- Kjær, E.D., McKinney, L.V., Nielsen, L.R., Hansen, L.N., Hansen, J.K., 2012. Adaptive potential of ash (*Fraxinus excelsior*) populations against the novel emerging pathogen *Hymenoscyphus pseudoalbidus*. *Evolut. Appl.* 5, 219–228. <https://doi.org/10.1111/j.1752-4571.2011.00222.x>.
- Kowalski, T., Holdenrieder, O., 2009. The teleomorph of *Chalara fraxinea*, the causal agent of ash dieback. *For. Pathol.* 39, 304–308. <https://doi.org/10.1111/j.1439-0329.2008.00589.x>.
- Langenbruch, C., Helfrich, M., Flessa, H., 2012. Effects of beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*) and lime (*Tilia spec.*) on soil chemical properties in a mixed deciduous forest. *Plant Soil* 352, 389–403. <https://doi.org/10.1007/s11104-011-1004-7>.
- Lenth, R., 2024. emmeans: Estimated Marginal Means, aka Least-Squares Means. In: R. Package Version 1 (10), 0.
- Liziniwicz, M., Tolio, B., Cleary, M., 2022. Monitoring of long-term tolerance of European ash to *Hymenoscyphus fraxineus* in clonal seed orchards in Sweden. *For. Pathol.* 52. <https://doi.org/10.1111/efp.12773>.
- Matisone, I., Matisons, R., Jansons, 2021. The struggle of ash—insights from long-term survey in Latvia. *Forests* 12, 340. <https://doi.org/10.3390/f12030340>.
- Maxwell, S.L., Fuller, R.A., Brooks, T.M., Watson, J.E., 2016. Biodiversity: The ravages of grass, nets and bulldozers. *Nature* 536, 143–145.
- McKinney, L.V., Nielsen, L.R., Collinge, D.B., Thomsen, I.M., Hansen, J.K., Kjær, E.D., 2014. The ash dieback crisis: genetic variation in resistance can prove a long-term solution. *Plant Pathol.* 63, 485–499. <https://doi.org/10.1111/ppa.12196>.
- Milford, A.B., Johansen, J., Kårstad, S., Schei, F.H., 2024. “Historical signs in the landscape”: ecosystem services, motivation and challenges of pollarding in Western Norway. *Agrofor. Syst.* <https://doi.org/10.1007/s10457-024-00994-9>.
- Mitchell, R., Hewison, R., Hester, A., Broome, A., Kirby, K., 2016. Potential impacts of the loss of *Fraxinus excelsior* (Oleaceae) due to ash dieback on woodland vegetation in Great Britain. *N. J. Bot.* 6, 2–15. <https://doi.org/10.1080/20423489.2016.1171454>.
- Mitchell, R.J., Beaton, J.K., Bellamy, P.E., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Gimona, A., Harmer, R., Hester, A.J., Hewison, R.L., Hodgetts, N.G., Iason, G.R., Kerr, G., Littlewood, N.A., Newey, S., Potts, J.M., Pozsgai, G., Ray, D., Sim, D.A., Stockan, J.A., Taylor, A.F.S., Woodward, S., 2014. Ash dieback in the UK: A review of the ecological and conservation implications and potential management options. *Biol. Conserv.* 175, 95–109. <https://doi.org/10.1016/j.biocon.2014.04.019>.
- Moe, B., 1995. Vernet edellovskog i Hordaland: tilstand, fastruteanalyser, floraoversikt og skjøtselbeov 20 år etter registreringene. Fylkesmannen i Hordaland, Miljøvernavdelinga.
- Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *J. Appl. Ecol.* 54, 12–27. <https://doi.org/10.1111/1365-2664.12669>.
- Morrison, L.W., 2021. Nonsampling error in vegetation surveys: understanding error types and recommendations for reducing their occurrence. *Plant Ecol.* 222, 577–586. <https://doi.org/10.1007/s11258-021-01125-5>.
- Needham, J., Merow, C., Butt, N., Malhi, Y., Matthews, T.R., Morecroft, M., McMahon, S. M., 2016. Forest community response to invasive pathogens: the case of ash dieback in a British woodland. *J. Ecol.* 104, 315–330. <https://doi.org/10.1111/1365-2745.12545>.
- Norwegian biodiversity information centre, 2021. Norways Red List for species 2021. <https://www.artsdatabanken.no/lister/rodlisterforarter/2021>.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., M. H., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Braak, C., Weedon, J., 2022. *vegan: Community Ecology Package*.
- Oostra, S., Majidi, H., Olsson, M., 2006. Impact of tree species on soil carbon stocks and soil acidity in southern Sweden. *Scand. J. For. Res.* 21, 364–371. <https://doi.org/10.1080/02827580600950172>.
- Paap, T., Wingfield, M.J., Burgess, T.I., Wilson, J.R.U., Richardson, D.M., Santini, A., 2022. Invasion Frameworks: a Forest Pathogen Perspective. *Curr. For. Rep.* 8, 74–89. <https://doi.org/10.1007/s40725-021-00157-4>.
- Pacheco-Riãno, L.C., Schei, F.H., Flantua, S.G.A., Grytnes, J.A., 2023. Lagging dynamics in the response of plant assemblages to global warming depends on thermal velocity. *Glob. Ecol. Biogeogr.* 32, 719–733. <https://doi.org/10.1111/geb.13653>.
- Pätsch, R., Jasková, A., Chytrý, M., Kucherov, I.B., Schaminée, J.H., Bergmeier, E., Janssen, J.A., 2019. Making them visible and usable—vegetation-plot observations from Fennoscandia based on historical species-quantity scales. *Appl. Veg. Sci.* 22, 465–473. <https://doi.org/10.1111/avsc.12452>.
- Piura, A., Lygis, V., Suchockas, V., Bartkevicius, E., 2011. Performance of Twenty Four European *Fraxinus excelsior* Populations in Three Lithuanian Progeny Trials with a Special Emphasis on Resistance to *Chalara Fraxinea*. *Balt. For.* 17, 17–34.
- Poland, T.M., McCullough, D.G., 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *J. For.* 104, 118–124.



- Potter, C., Harwood, T., Knight, J., Tomlinson, I., 2011. Learning from history, predicting the future: the UK Dutch elm disease outbreak in relation to contemporary tree disease threats. *Philos. Trans. R. Soc. B-Biol. Sci.* 366, 1966–1974. <https://doi.org/10.1098/rstb.2010.0395>.
- Przybyl, K., 2002. Fungi associated with necrotic apical parts of *Fraxinus excelsior* shoots. *For. Pathol.* 32, 387–394. <https://doi.org/10.1046/j.1439-0329.2002.00301.x>.
- Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., 2017. No saturation in the accumulation of alien species worldwide. *Nat. Commun.* 8, 14435. <https://doi.org/10.1038/ncomms14435>.
- Semizer-Cuming, D., Chybicki, I.J., Finkeldey, R., Kjær, E.D., 2021. Gene flow and reproductive success in ash (*Fraxinus excelsior* L.) in the face of ash dieback: restoration and conservation. *Ann. For. Sci.* 78. <https://doi.org/10.1007/s13595-020-01025-0>.
- Skovsgaard, J.P., Wilhelm, G.J., Thomsen, I.M., Metzler, B., Kirisits, T., Havrdová, L., Enderle, R., Dobrowolska, D., Cleary, M., Clark, J., 2017. Silvicultural strategies for *Fraxinus excelsior* in response to dieback caused by *Hymenoscyphus fraxineus*. *For.: Int. J. For. Res.* 90, 455–472. <https://doi.org/10.1093/forestry/cpx012>.
- Solstad H.E.R., Arnesen G., Eidesen P.B., Gaarder G., Hegre H., Høitomt T., Mjelde M., Pedersen O., 2021. Karplanter: Vurdering av ask *Fraxinus excelsior* for Norge. In: Artsdatabanken (Ed.), *Rodlista for arter*.
- Talgå, V., Sletten, A., Brurberg, M.B., Solheim, H., Stensvand, A., 2009. *Chalara fraxinea* isolated from diseased ash in Norway, 548-548 *Plant Dis.* 93. <https://doi.org/10.1094/pdis-93-5-0548a>.
- Timmermann, V., Børja, I., Hietala, A., Kirisits, T., Solheim, H., 2011. Ash dieback: pathogen spread and diurnal patterns of ascospore dispersal, with special emphasis on Norway. *EPPO Bull.* 41, 14–20.
- Timmermann, V., Nagy, N.E., Hietala, A.M., Børja, I., Solheim, H., 2017. Progression of ash dieback in Norway related to tree age, disease history and regional aspects. *Balt. For.* 23, 150–158.
- Timmermann, V., Børja, I., Clarke, N., Gohli, J., Hietala, A.M., Jepsen, J.U., Krokene, P., Haga, H.L., Nagy, N.E., Nyeggen, H., Solberg, S., Solheim, H., Solvin, T., Svensson, A., Tollefsrud, M.M., Vindstad, O.P.L., Økland, B., Aas, W., 2023. Skogens helsetilstand i Norge. Resultater fra skogskadeovervåkingen i 2022. Nibio Rapport.
- Verheyen, K., Bazány, M., Checko, E., Chudomelová, M., Closset-Kopp, D., Czortek, P., Decocq, G., De Frenne, P., De Keersmaecker, L., Enríquez García, C., Fabciová, M., Grytnes, J.A., Hederová, L., Hédli, R., Heinken, T., Schei, F.H., Horváth, S., Jaroszewicz, B., Jermakowicz, E., Klinerová, T., Kolk, J., Kopecky, M., Kuras, I., Lenoir, J., Macek, M., Máliš, F., Martinussen, T.C., Naaf, T., Papp, L., Papp-Szakály, A., Pech, P., Petrik, P., Prach, J., Reczynska, K., Sætersdal, M., Spicher, F., Standovář, T., Swierkosz, K., Szczesniak, E., Tóth, Z., Ujházy, K., Ujházyová, M., Vangansbeke, P., Vild, O., Wolkowycy, D., Wulf, M., Baeten, L., 2018. Observer and relocation errors matter in resurveys of historical vegetation plots. *J. Veg. Sci.* 29, 812–823. <https://doi.org/10.1111/jvs.12673>.
- Wulf, M., Naaf, T., 2009. Herb layer response to broadleaf tree species with different leaf litter quality and canopy structure in temperate forests. *J. Veg. Sci.* 20, 517–526. <https://doi.org/10.1111/j.1654-1103.2009.05713.x>.
- Zhao, Y.J., Hosoya, T., Baral, H.O., Hosaka, K., Kakishima, M., 2012. *Hymenoscyphus pseudoalbidus*, the correct name for *Lambertella albida* reported from Japan. *Mycotaxon* 122, 25–41. <https://doi.org/10.5248/122.25>.
- Zheng, H.D., Zhuang, W.Y., 2014. *Hymenoscyphus albidoides* sp. nov. and *H. pseudoalbidus* from China. *Mycol. Prog.* 13, 625–638. <https://doi.org/10.1007/s11557-013-0945-z>.