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Risk factors of ash dieback disease and consequences for carbon storage in natural ash populations

Rachel Mailes [a,b,*], Bruno B.L. Cintra [a,b,c], Rodrigo S. Bergamin [a,b,d], Laura J. Graham [a,b,e], Estrella Luna [b,f], Matthew S. Heard [g,h], Thomas J. Matthews [a,b,i], A. Robert MacKenzie [a,b], Roel Brienen [j], Adriane Esquivel-Muelbert [a,b,d]

[a] School of Geography, Earth and Environmental Science, University of Birmingham, United Kingdom
[b] Birmingham Institute of Forest Research (BIFoR), University of Birmingham, United Kingdom
[c] Norbury Park Estate, Staffordshire, England, United Kingdom
[d] Department of Plant Science, University of Cambridge, United Kingdom
[e] Biodiversity, Ecology & Conservation Group, International Institute for Applied Systems Analysis, Vienna, Austria
[f] School of Biosciences, University of Birmingham, Birmingham B15 2TT, United Kingdom
[g] National Trust, Heelis, Kemble Drive, Swindon SN2 2NA, United Kingdom
[h] Centre for Rural Policy Research, University of Exeter, Exeter, Devon, United Kingdom
[i] CE3C – Centre for Ecology, Evolution and Environmental Changes, Azorean Biodiversity Group, CHANGE – Global Change and Sustainability Institute and Universidade dos Açores – Faculty of Agricultural Sciences and Environment, Angra do Heroísmo, Açores 9700-042, Portugal
[j] School of Geography, University of Leeds, United Kingdom

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ABSTRACT

Ash (*Fraxinus excelsior*) is one of the most dominant species in UK broadleaved woodlands, contributing up to 10 million tonnes of national carbon stock. However, it is currently threatened by ash dieback disease (*Hymenoscyphus fraxineus*). Despite the pervasiveness of this pathogen, its impact on forests' capacity to mitigate global change and the factors influencing symptom severity and mortality of infected trees are poorly understood. Analysing 40 years of data on ash dynamics, we assess impacts of ash dieback on the demography and carbon stocks of five natural populations. We further investigate risk factors for developing severe ash dieback symptoms or mortality. We observed an 8.7 % reduction in ash population numbers since previous surveys and a significant increase in mortality rates of small trees. There has been no significant increase in carbon stocks within ash populations since the conformation of ash dieback in the UK in 2012. Large trees have a decreased risk of mortality from ash dieback, while number of ash neighbours increased the risk. The severity of dieback symptoms decreased with increasing neighbourhood basal area and light availability. Trees with severe dieback symptoms hold 27.4 % of total carbon stored by ash trees, constituting a committed carbon loss or debt within these forests. Together, our results highlight the importance of stand density and light competition in modulating symptom severity and mortality of infected ash trees. We also suggest that the carbon debt within living, but fatally infected ash, requires consideration when calculating carbon mitigation capacities of effected forests.

1. Introduction

The number of invasive pathogen introductions and species they threaten is rising across the world due to trade globalisation and climate change (Fisher et al., 2012; Jönsson and Thor, 2012; La Porta et al., 2008; Needham et al., 2016). One species facing such a pathogen outbreak is the European common ash (*Fraxinus excelsior*), vulnerable to the invasive ascomycete fungus *Hymenoscyphus fraxineus*, which causes ash dieback disease (Baral et al., 2014; Gross et al., 2014; Nielsen et al., 2017; Pautasso et al., 2013). *F. excelsior* is a common and widespread pioneer and mature woodland tree species in temperate Europe, however, within the last 30 years, mortality of ash has risen to 70 % in natural woodlands across mainland Europe and southeast England (Coker et al., 2019). This has sparked concern over the species' capacity to mitigate global climate change (Marçais et al., 2022) and highlighted the importance of understanding the future of this species and the

* Corresponding author at: School of Geography, Earth and Environmental Science, University of Birmingham, United Kingdom.
E-mail address: Rxm508@student.bham.ac.uk (R. Mailes).

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related impacts on carbon stocks. In Britain alone, ash contributes 12 % of broad-leaf forest cover, storing 10 million tonnes of carbon (Forestry Research, 2020), and supporting 953 other species, 44 of which would become co-extinct with the loss of this species (Mitchell et al., 2014). Ash is also considered an important tree species in the UK as it provides many ecosystem services including increasing landscape connectivity due to its success as a hedgerow species, which makes it popular with landowners and the public (Marzano et al., 2019). Given this importance, the loss of ash will have both cultural and environmental consequences. However, no clear estimate yet exists for the full effect of mortality of this species.

It is known that some resistant or minimally infected trees do survive ash dieback (Enderle et al., 2019; Metheringham et al., 2025), however the factors driving resistance are still debated. Historically, greater tree diversity has provided woodlands with greater resilience to diseases by reducing both the speed of transmission and severity of symptoms in infected trees (Roberts et al., 2020). Mixed species woodlands can have less intense ash dieback infections (Lévesque et al., 2023; Martin et al., 2025), potentially due to the chemical composition of fallen leaves in diverse woodlands facilitating faster decomposition of ash leaves, thus reducing the volume of *Hymenoscyphus* spores produced in the leaf litter (Havrdová et al., 2017). The species identity of neighbouring trees can also influence the severity of dieback in an individual; for example, severity of ash dieback symptoms in forests in the Czech Republic were positively correlated with the presence of oak, beach, pine or birch (Havrdová et al., 2017). This effect of neighbours is yet to be investigated in natural mature woodlands in the UK.

Similarly, ash dieback symptom severity increases with proximity and infection severity of the closest monospecific ash stand, which acts as a large source of infection (Cracknell et al., 2023; Grosdidier et al., 2020). It is believed that infection by a high density of spores is required to cause significant dieback symptoms in a tree (Grosdidier et al., 2020). Therefore, proximity of infected stands likely increases the atmospheric spore load sufficiently to cause increased symptoms in surrounding ash trees. However, others have suggested that the effect of nearby ash stands on infection severity of an individual ash tree may be caused by competition effects between the conspecific trees (Cracknell et al., 2023). Evidence for the effect of density on the intensity of ash dieback is still contested, with some studies finding no relationship between ash density or total tree density, and dieback severity or mortality rates (George et al., 2022). This uncertainty hampers the creation of more effective management and mitigation practices to protect the future of ash populations and their associated species.

Tree characteristics and their local environment also seem to be linked to ash dieback related mortality. Tree size has been found to influence the susceptibility of a tree to ash dieback (Enderle et al., 2019; Grosdidier et al., 2020). This can be explained due to smaller trees' branches being closer to the ground and therefore closer to the source of *H. fraxineus* spores (Combes et al., 2024). Other factors contributing to the greater susceptibility of smaller trees include their reduced woody tissue defenses, the greater speed at which stem girdling can occur, and the reduced area of leaf infection required to fatally impact their photosynthetic capacity (Combes et al., 2024). As small trees also have less surface area for photosynthesis, loss of any leaf area results in an insufficient amount of sugar being produced (Klesse et al., 2021; Nielsen et al., 2022). This can be aggravated by the reduction of early wood vessel production in infected trees, further compromising water transport through the phloem and thus their photosynthetic capacity (Klesse et al., 2021; Nielsen et al., 2022). However, changes in mortality rates for different size classes since the introduction of ash dieback have not been calculated for the UK.

Fungi infecting fallen ash leaf litter in open sun-lit areas seem to produce less apothecia (the fruiting body of *H. fraxineus*) when compared to those under shade (Inoue et al., 2019). Therefore, trees with more open understories should be exposed to smaller spore loads than light-suppressed trees, resulting in fewer infections. This will also reduce their probability of mortality as re-infection over subsequent years is a known factor which increases ash mortality. Alternatively, the lack of apothecial production in light-exposed fungi may indicate non-optimal conditions for the pathogen, impacting its virulence and ability to cause severe symptoms in host trees. A potential driver for this is temperature, as *H. fraxineus* is known to have an upper survival threshold of *c.* 36°C in plant tissue submerged in water, and to halt all growth in air temperatures > 28°C (Hauptman et al., 2013). Additionally, trees within a forest with lower average canopy temperature have more severe ash dieback infections than those in open habitats with higher average canopy temperatures. Increasing canopy gaps has been found to significantly reduce ash dieback establishment and development (Grosdidier et al., 2020). However, to date no assessment had been conducted on how interactions between tree size, light exposure, and local environment may drive symptom severity and subsequent mortality of infected ash trees.

Here we investigate the impacts of ash dieback in Great Britain's mature woodlands and the characteristics of the trees and their local conditions which lead to high ash dieback severity and tree death. We investigated how mortality rates and carbon stocks have changed since the introduction of ash dieback to the UK and which environmental and neighbourhood variables are associated with the symptom severity and mortality likelihood of ash trees. We expect to see an increase in ash mortality rates, particularly affecting larger trees, leading to a decrease in carbon stocks within ash since the introduction of ash dieback disease. We further anticipate that a high proportion of ash are highly infested, leading to a 'carbon debt' across UK forests whereby a large proportion of living carbon is stored within ash committed to succumb to ash dieback within the coming years. This concept of committed carbon debt is analogous to that of committed climate change and global temperature rise that will occur as climate equilibrium is achieved from the atmospheric CO_2 released to date (Matthews and Weaver., 2010). We also hypothesise that neighbourhood variables related to high stem density will exacerbate symptom severity and increase mortality likelihood of ash trees, and that variables related to high stand diversity, high light availability and low neighbourhood competition will have positive impacts on dieback resistance and survival of ash trees.

2. Methods

We use a unique data set collected in five mature woodlands across the UK; distributed across Southern England, Northern England and Scotland. Average annual temperature and precipitation in these sites range from 7.4°C to 10.4°C, and 538 mm to 1364 mm respectively, representing a range of climatic conditions within the envelope of temperate forest climates (Sommerfeld et al., 2018). Species composition varies between oak and/or beech- dominated sites in southern England and Scotland and an ash-dominated site in northern England.

2.1. Data collection

Between two and eight permanent transects of varying length are located within continuous sections of mature woodlands in each site. These transects vary in area, ranging from between 0.36 and 1.7 ha per site, totalling a combined survey area of 5.4 ha. Each transect is divided into a series of 30 × 20 m sections with 10 m either side of a central transect line. The number of sections, and therefore the length of the transect, varies between sites from 180 to 900 m. Each site has between one and three previous surveys of these transects from 1961 to 2014 (SI Table 1). We re-surveyed all sites between May and October 2022 creating a data set of 17 censuses, nested within five sites.

In each transect, all living stems with diameter ≥ 5 cm were measured at 1.3 m, diameter at breast height (dbh), using a standard diameter tape measure. In the presence of features such as scars or forks at 1.3 m, the point of measurement (POM), was moved to at least 20 cm above or below the outer limits of such features. The dbh of standing dead trees were also measured; including those that were dead in previous surveys. A subplot was located 2 m either side of the central line, covering 20 % of the total plot area, in which regeneration measurements were taken – dbh of all saplings 1.5–4.9 cm at 1.3 m. Additional data recorded included the species identity, tree status, and health of each tree. When morphological similarities made species differentiation uncertain between *Quercus petrea* and *Quercus robur* and *Betula pendula* and *Betula pubescens*, these were recorded as *Quercus spp* and *Betula spp* respectively. Tree status was defined as binary: i.e., dead or alive. Trees were considered dead when they were uprooted or the trunk was broken, with no evidence of resprouting in either case, or when the canopy of standing trees had produced no leaves or buds and the cambium was shown as dead. Trees that were previously recorded and could not be located at the same coordinates were also assumed dead. Tree health and environment, such as light availability and canopy damage, were recorded using score and flag-based systems from the RAINFOR protocol (Moravie et al., 1999). Briefly, light availability was scored between one and five, with one as an understory tree with no direct light and five as an emergent tree with complete access to direct light. Canopy damage was also scored between zero and four with zero as no crown damage and four as more that 75 % crown lost (Phillips and Baker, 2001). Symptoms of ash dieback were recorded using an eight-point score system based on that by Pliûra et al. (2011). The scores were grouped as: 0. No Symptoms; 1. Signs of minor infection; 2. Up to 25 % canopy loss; 3. 26–50 % canopy loss; 4. 51–75 % canopy loss; 5. 76–100 % canopy loss; 6. 100 % canopy loss and healthy epicormic resprouts; 7. 100 % canopy loss and infected epicormic resprouts; 8. Dead (SI, Fig. 1). The symptoms were scored on all ash trees, except for 197 in Colt Park that were unable to be assessed due to early leaf shed. These unscored trees were excluded from the symptom analysis.

2.2. Data processing

We did not consider woodland with evidence of direct human disturbance such as paths, fences or logging, therefore disturbed transect sections were removed. In total we removed eight sections across two sites: Clairinsh (0.19 ha) and Langley (0.24 ha). Annual tree mortality (M) was calculated following Kohyama et al. (2017):

$$M = 1 - \left(\frac{S}{N_i}\right)^{\frac{1}{t}} \tag{1}$$

Where S is the number of survivors, N_i is the number of stems in the survey at the beginning of each interval and *t* is the time interval between two sampling dates. The mean annual mortality rate was then calculated for sample intervals before and after 2012, when the first confirmed case of ash dieback occured in the UK (Plumb et al., 2020). The change in mortality rate was calculated by comparing the difference between these rates, for the total population and for three different size classes (all trees, saplings ($1 \leq$ dbh <5 cm), small trees ($5 \leq$ dbh $<$ 20 cm), and large trees (≥ 20 cm dbh)). The year 2012 was used as this is the official date of ash dieback presence confirmation in the UK (Plumb et al., 2020), however, some records suggest that the disease was in fact introduced as early as the 2000s (Wylder et al., 2018).

In the absence of data from the more accurate Terrestrial Laser Scanning method, above ground biomass (AGB) was calculated using species-specific allometric equations from the *allodb* R package (Gonzalez-Akre et al., 2022) based on measured diameter. Height measurements were not available for all trees; therefore, we were unable to include this variable in the calculations. This prevents the capture of specific details about carbon stock variation between sites, however the climatic range across our sites would create a smaller variation in the height-dbh relationship than the error within height estimation itself (Fortin et al., 2019); and as this study assesses the within site carbon trends rather than between sites, it is not limited by this factor. The standard value for carbon as a fraction of AGB in temperate forests is 47 % (IPCC et al., 2006, Table 4.3), therefore carbon stocks were estimated by multiplying AGB by 0.47. Relative growth rate was also estimated using the annual growth of the tree, relative to its size.

To understand the impact of neighbourhood variables on infection severity and mortality risk, we generated a series of variables that characterise key parameters of the neighbourhood's structure and composition, using a buffer of 5 m around each focal tree. These variables included: number of ash neighbours; total basal area of neighbour trees; neighbourhood diversity; and neighbourhood competition level. A 5 m buffer was selected due to the narrow nature of the transect (20 m width); any buffer wider than 5 m would have excluded many individuals within the transect and so resulted in a significantly smaller data set. To test the effect of buffer size on our results, a sensitivity analysis was conducted to assess if significant variables maintained their effects with a buffer of 7.5 m, which produced a reduced data set of roughly half (SI figure 7 & 8). Buffers greater than this resulted in a data set of only 2 individuals and could not be tested. However, as our methods were designed to understand the effect of neighbourhood influences on mortality and severity, using the 5 m buffer data was still possible. Assessing neighbourhood at larger scales, while not possible with our sampling design, might allow for understanding the influence of neighbourhood on disease dispersal rate and is an important area for future research. The R packages used to derive these variables were *spatstat* (Baddeley et al., 2015), *vegan* (Oksanen et al., 2024), and *TreeCompR* (Rieder et al., 2024).

Neighbourhood biodiversity was calculated using the Shannon-Wiener diversity index (H):

$$H = -\sum_{i=1}^{n} p_i \log(p_i) \tag{2}$$

Where p_i is the proportional abundance of species *i,* and *i* ranges from 1 to *n*, the total number of species in the transect.

Neighbourhood competition pressure was calculated using the Hegyi competition index (CI) (Hegyi, 1974):

$$CI = \sum_{j=1}^{N} \delta_j \frac{DBH_j}{DBH_i} \tag{3}$$

Where DBH_i is the diameter of the focal tree, and DBH_j is the diameter of each of *N* competitor trees at distances δ_j from the focal tree.

To conform to our binomial analysis (see below), the severity scores for ash dieback symptoms were simplified, with those scoring four or less on our eight-point system classed as 'not severe' and those with scores of five or greater classed as 'very severe'. This produced two categories of ash that had either ≥ 75 % or < 75 % canopy loss from dieback. This threshold of canopy loss was the closest value within our scoring system to available estimations in the literature, as trees are not known to recover beyond such loss (Hibben and Silverborg, 1978), yet the exact point at which individuals become terminally infected is unknown. As with the dieback severity, light exposure was also converted from the 1–5 RAINFOR scores (Moravie et al., 1999), so that those trees with light exposure scores of 1–3A were 'suppressed' and those with scores of 3B-5 were 'not suppressed'.

2.3. Statistical analysis

To understand the impact of ash dieback at the population level we used a Wilcoxon signed rank test to compare mortality rates within the ash population before and after the introduction of ash dieback in 2012 (Clark and Webber, 2017). This was done for all sites except Colt Park as there have been only two sampling efforts there, preventing this calculation. As ash dieback is known to progress more rapidly in small trees, we grouped the tests by tree dbh to assess how much variation in mortality rate change was explained by tree size class. Further Wilcoxon tests were used to assess if mortality rate change of the ash populations differed significantly from that of the other species present. The comparison with non-ash species enabled identification of ash-related mortality that varied significantly from background mortality caused by other factors such as overgrazing and climatic events. The difference between carbon stock assimilation before and after the introduction of ash dieback was also tested for significance using a paired Wilcoxon test. This was conducted for total ash-based carbon stocks as well as by size class, including saplings, small trees, and large trees with the same class boundaries as used in the mortality tests.

To understand the drivers of variation in ash tree symptom severity and mortality, two generalized linear mixed models (binomial) with logit link function were fitted using the R package *lmer4* (Bates et al., 2015) with the response variables: ash tree mortality and severity of ash dieback symptoms (SI Eq. 1 & 2). Predictor variables were the number of ash neighbours, neighbourhood biodiversity, total neighbourhood basal area, neighbourhood competition pressure, and focal tree diameter. In the symptom severity model, light exposure of the focal tree was also included along with interactions between light and focal tree diameter and number of ash neighbours. These interactions were added due to an observed shift in the slope of the correlation between symptom severity and ash neighbours/tree diameter in the suppressed and not suppressed light classes. Focal tree diameter was used in the model rather than focal tree growth due to the lack of multiple diameter measurements for some trees in the data set, meaning growth could only be calculated for a subset of the trees and the models were too complex to converge with the reduced data set. All other predictors were included in the models, with scaling required to allow comparability between variables. Both models also used site as a random effect (random intercept). We used the *Dharma* package (Hartig, 2024), to check the assumptions of both models were met and tested for spatial autocorrelation by plotting residuals and running Moran's I test.

3. Results

Ash trees were present in surveys before and after the introduction of dieback in 9 out of 12 transects spread across five sites. Overall, the number of ash trees in our study decreased by 8.7 %, from 658 in previous surveys (1989 – 2008) to 601 trees in 2022. Despite the reduction in ash tree number, ash stem mortality rates across sites have not changed significantly when comparing the period prior and post 2012 ($V = 29$, $P > 0.05$). The difference in mortality rates pre and post 2012 in ash did not differ from that calculated for the other species present (Fig. 1A). When repeating this analysis only for the small size class (5–20 cm dbh) we find that mortality rates significantly increase for ash post 2012 ($V = 36$, $P < 0.01$) and that this increase is significantly greater than the trend observed for small trees of all other species present ($W = 18$, $P < 0.05$, Table S2) (Fig. 1C). A sensitivity analysis showed consistent trends with varying significance when removing a transect from the Buckholt site that was observed to be an outlier, with a large decrease in mortality in the census interval ending in 2022 (Table S2).

Site-level change in the ash population mortality rates varied between –4.1 and 5.0 %, compared to a range of –0.3–3.6 % for all other species analysed together (Fig. 1A). The greatest variation was seen in the sapling size class with ash mortality rate changes between −11.9 and 10.5 % after 2012, compared to a rate change of –4.6–6.1 % for all other species together (Fig. 1D).

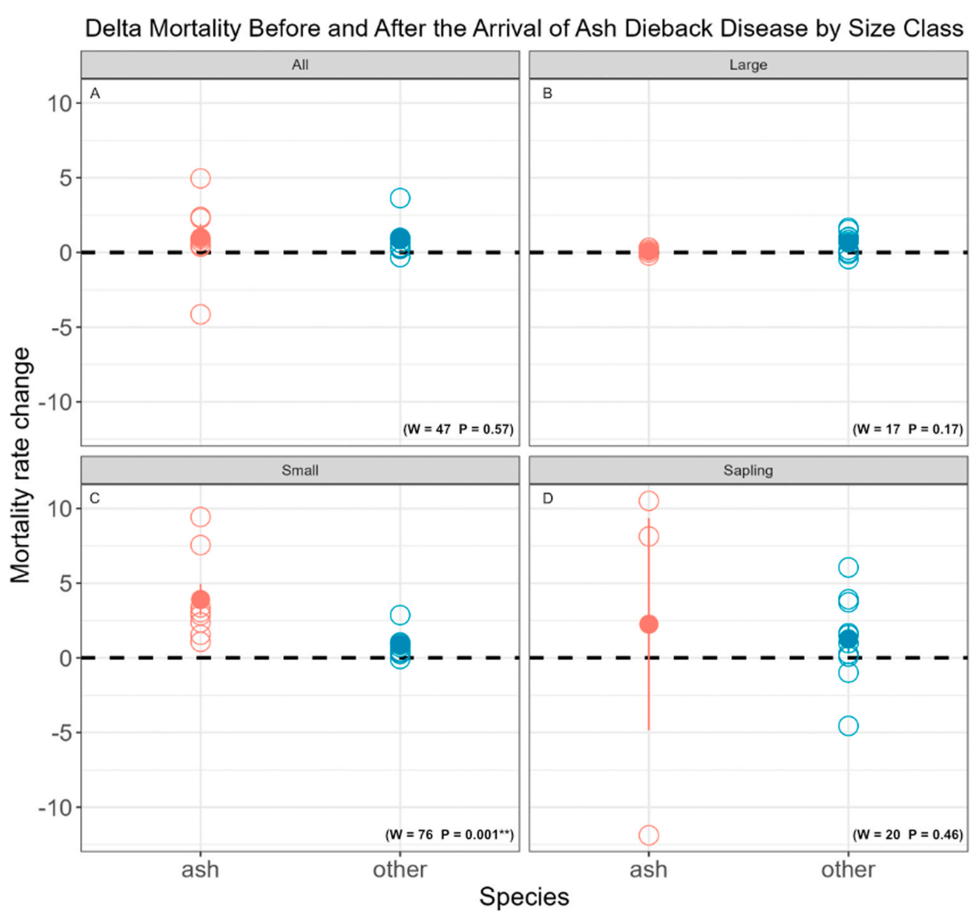

Fig. 1. Rate change of ash and other species mortality since 2012 when ash dieback was introduced to the UK. The y-axis shows the mean difference (closed circles) between pre and post 2012 mortality rate across different transects (open circles) for ash (pink) and all species together (blue). This analysis was repeated for all stems (A), and different size classes, Large: > 20 dbh (B); Small: 5–20 dbh (C); and Sapling: 1.5–5 dbh (D).

3.1. Consequences for carbon

Despite a steadily increasing trend in carbon stored within ash trees across all sites (SI Figure 2) over the 40-year period of this study (Fig. 2), we find no significant difference in stocks before and after 2012 ($W = 64$, $P > 0.5$). We found that on average trees with > 75 % canopy loss to ash dieback hold just under a third (27.4 %) or 20.7 Mg of the carbon stocked by ash trees. However, this proportion of highly infected ash varies widely, from 4.2 % to 76.9 %, across sites (Fig. 2).

3.2. Drivers of ash dieback mortality and severity

Our comparison of standardised model coefficients show that mortality probability increases with the numbers of ash neighbours and decreases with size of the focal ash (Fig. 3A). The fixed effects have high explanatory power, while the random effect of site adds little extra power ($R^2m = 0.81$, $R^2c = 0.88$) (Fig. 3A). We did not find a significant effect of neighbourhood basal area, tree species richness, or competitive index on mortality likelihood of ash trees.

Of the 404 ash trees scored for ash dieback, only one (0.3 %) showed no symptoms of ash dieback disease. The severity of these infections was negatively associated with light exposure of focal ash trees but positively associated with total basal area of the neighbourhood (Fig. 3B). The fixed effects of the severity model have less explanatory power than the mortality model, and again the random effect of site adds little extra power ($R^2m = 0.25$, $R^2c = 0.28$) (Fig. 3B). The negative association with basal area was also found when ash basal area effects were investigated at the transect level (SI Figures 11 & 12).

No deviations from the expected distributions and no evidence of spatial autocorrelation were found when testing the validity of either model with plots (SI Figures 3 & 4) or Moran's I tests (SI Figures 5 & 6). A further analysis was also performed to assess if the significant variables maintained their effect at a wider buffer range (7.5 m) despite a smaller data set. No results differed for the mortality model; however, the effect

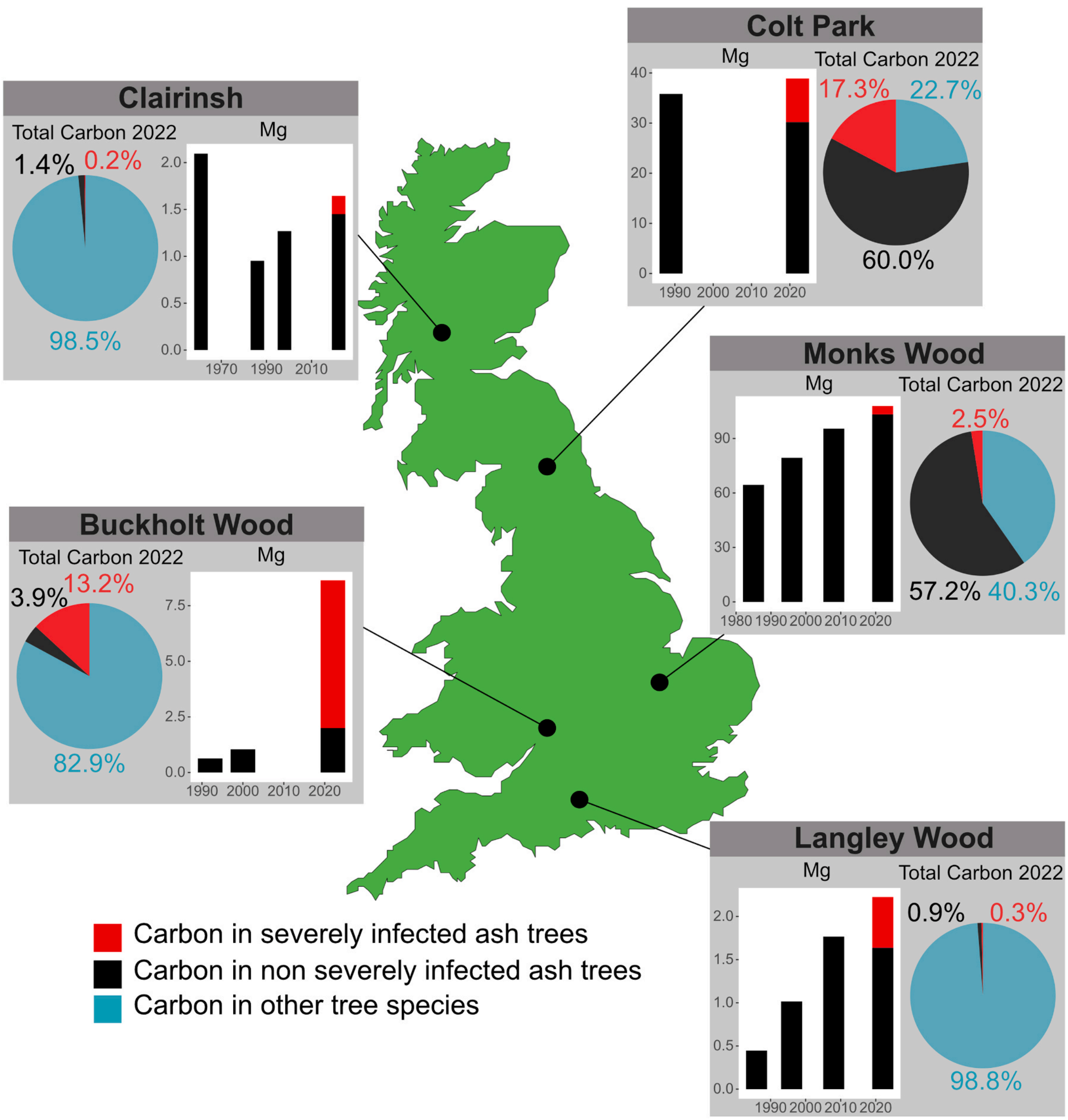

Fig. 2. Impact of ash dieback on carbon stocks. Bar charts show trends in carbon stocks (Mg) within the ash trees over time for each site. The pie charts represent the distribution of the total carbon stocks across trees in 2022 within the mature woodlands studied. Red represents stocks in trees with > 75 % canopy loss to ash dieback in the latest census (2022), black shows carbon in ash trees with < 75 % canopy loss to ash dieback, and carbon stocks in species other than ash are shown in blue.

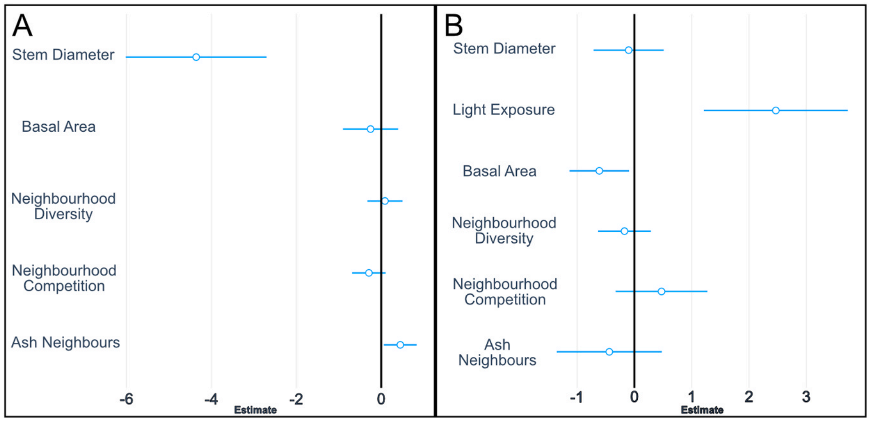

Fig. 3. Risk factors of ash dieback on the likelihood of ash tree mortality (A) and on likelihood of development of severe dieback symptoms (B). Plots show scaled coefficients for each variable explaining likelihood of death (A) and symptom severity variation (B) in ash trees.

of neighbourhood basal area on ash dieback symptom severity was lost (SI Figures 7 & 8).

4. Discussion

We assessed long-term data across five mature woodlands to understand the impact of ash dieback on natural ash populations. Despite identifying declines in total population sizes in the studied mature woodlands, overall population mortality rates are not significantly greater since the introduction of ash dieback (Fig. 1A), and overall carbon stocks in ash trees have continued to increase (Fig. 2). This suggests that these forests are in a lag phase, where the mortality impacts of ash dieback disease in larger trees are still developing and therefore, do not yet show increases in mortality. At the same time the continued growth of surviving ash trees has offset the loss of carbon from mortality of the smaller trees. These trends in mortality and carbon stocks during the identified lag phase highlight the need to understand this disease better in order to make more accurate predictions for the future of ash trees and their associated carbon stocks and biodiversity. As a first step towards this, we have identified that tree size and number of ash trees within 5 m of an individual have a significant effect on mortality likelihood. We have also found light suppression to cause increased symptom severity in trees and increased neighbourhood basal area to have the opposite effect. These factors can help to predict the likelihood of individual trees resisting ash dieback or succumbing to it.

We observed an 8.7 % decrease in ash population size across all our sites but no significant change in mortality rates since the official confirmation of ash dieback in the UK (2012) and no significant deviation from the mortality rates of other species present (Fig. 1A). However, the mortality rate for small trees and saplings did increase significantly, also differing significantly from the mortality of other species in this size class (SI Table 2). This supports the conclusions of earlier work which found small ash trees are more susceptible to the disease (Combes, 2022; Cracknell et al., 2023). Additionally, further research suggests that the infection period of this study (10 years) is not long for large trees and it is to be expected that they would not have succumbed to the disease within this time (Marçais et al., 2017). Therefore, longer-term studies are needed to understand the end population impacts of ash dieback.

The site-level mortality patterns did not seem to be related to assumed durations of infection, which based on available records, is likely to be longest in the south of the UK. However, more detailed analysis of this was not possible as reliable estimates for the date of ash dieback arrival in each site were unavailable. Due to the lack of exact infection dates for each site, the estimated date of 2012 was used for these analyses, and therefore caution should be taken when interpreting these results as it is likely the disease was present earlier in some sites (Wylder et al., 2018). Additional uncertainty is present due to the varying time periods available for historic data in these sites and the possibility of other factors such as climate change driving changes in mortality during this period. However, as the mortality rate changes we observe are also significantly different to that of other species (Fig. 1), they are likely to be a result of a variable with greater influence on ash trees rather than climate change, which effects many species simultaneously. Further studies, using sites with records of infection duration for each tree with data available for similar years/timespans will be valuable in providing more details into the impact of infection length on forests.

Surprisingly, ash-based carbon stocks increased throughout the study period. This may suggest that these forests are still recovering from past disturbances such as management or even the natural replacement of elm (*Ulmus procera*) populations after their losses to Dutch elm disease (*Ophiostoma novo-ulmi*), however detailed site histories are unavailable to confirm this. On average, in our sites nearly one third (27.4 %) of these stocks are contained in trees that are very severely infected by ash dieback (Fig. 2). This provides further evidence that these forests are in a lag phase where there is a carbon debt in effect committed by the future increased mortality of, and carbon losses from, highly infected trees. We define carbon debt in this paper as carbon within very severely infected ash trees that are unlikely to recover and will eventually be lost to the disease.

In addition to the diseased trees expected to die, the allometric equations used to calculate carbon stocks are made for healthy trees and are unlikely to capture the high-level crown damage (Kim et al., 2017) caused by ash dieback. Therefore, very severely infected trees have likely already lost some of their carbon and will continue to slowly release it over the course of their decline and eventual death. Given the pervasiveness of ash dieback, we suggest that carbon budget policies should consider that aboveground biomass is likely to be overestimated for woodlands with ash dieback. Our estimations are based on a 75 % threshold of canopy infestation as a point of no return for infected trees (Hibben and Silverborg, 1978). However, research on the length of infection prior to death, amount of carbon loss in the crown during this period and infection severity after which individuals do not recover is still needed to understand the full extent of the carbon debt caused by this disease. The number of highly infected trees we observe is currently lower than the predicted total eventual loss: up to 70 % population in natural woodlands (Coker et al., 2019) and therefore will only increase in the future. The vulnerable carbon we identify also represents a large margin for error in stock estimations and future predictions for any woodland effected by diseases with a long duration before mortality. Additional research will be required to identify other diseases that kill trees with similar drawn-out infection periods prior to mortality, creating carbon debts in other tree species and forests.

4.1. Risk factors of ash dieback severity and mortality

Prior studies indicate that less dense and more diverse stands have reduced mortality by ash dieback and that mortality is higher in smaller trees (Cracknell et al., 2023; Enderle et al., 2019; Grosdidier et al., 2020; Lévesque et al., 2023; Martin et al., 2025). We found no evidence that mortality likelihood is influenced by total neighbourhood density or tree species richness. However, we find that greater numbers of ash neighbours do increase the likelihood of mortality (Fig. 3A). This is somewhat consistent with the findings that ash mortality increased with proximity to the nearest ash stand in Lady Park Wood, Gloucestershire (Cracknell et al., 2023) and that increased stand and host density resulted in greater ash dieback levels for forests in France (Grosdidier et al., 2020; Martin et al., 2025). The effect of conspecific neighbours on ash tree mortality is consistent with our hypothesis that variables related to neighbourhood density would increase mortality likelihood, as ash trees in more densely populated ash stands have greater mortality likelihood. Drivers of this effect could be either the greater spore exposure or the effect of intra-specific competition for light, water and resources (Cracknell et al., 2023). In line with prior studies, small trees in our sites also have greater likelihood of mortality (Fig. 3A) (Combes et al., 2024; Cracknell et al., 2023; Hibben and Silverborg, 1978).

Light-availability and, contra-intuitively, basal area of the neighbourhood reduced the likelihood of an ash tree having severe dieback symptoms (Fig. 3B). These opposing results suggest different mechanism are influencing the trees. Firstly, the negative effect of basal area on symptom severity might reflect the fact that saplings, more vulnerable to ash dieback (Fig. 3A) (Combes et al., 2024; Cracknell et al., 2023; Hibben and Silverborg, 1978), are likely to be found grouped together in canopy gaps, where total basal area is smaller. It should also be noted that isolated trees may simply be those that have survived the infection long enough for others within their neighbourhood to have died, leaving the survivors in less dense and more open canopy positions in the forests. This process may not have been captured in our study due to the long intervals between sampling efforts. Secondly, under low light-availability, reduced photosynthetic capacity could lead to greater vulnerability to ash dieback due to lack of resources for defence (Combes et al., 2024). Alternatively, or additionally, high-light availability might decrease exposure to the pathogen as apothecia production is known to decrease in leaf litter under high light exposure (Inoue et al., 2019), generating less spores in open canopy forests. Direct sunlight and its effect on tree canopy microclimate has also previously been associated with reduced ash dieback infection between trees in forests and in isolation (Hauptman et al., 2013). Combined with our study, such prior work on the effect of temperature highlights the importance of microclimate on ash dieback. Future research should focus on understanding this interaction between different environmental drivers and whether and how they can be used to mitigate the effects of dieback. The effect of temperature also presents the possibility of reduced infection rates and severity of ash trees under rising atmospheric temperatures due to climate change (Hauptman et al., 2013).

4.2. Implications

Our new understanding of ash dieback disease on population dynamics in mature woodlands has potential implications for management and conservation. Firstly, as ash mortality rates increased with the number of ash neighbours, we suggest that mixed stands are the most beneficial forest type in which to grow ash. Secondly, as symptoms decreased with higher basal area and increased light exposure, we suggest open canopy areas would also be beneficial for infected ash growth. To achieve this for young ash stands showing signs of severe dieback infections, thinning the most severely affected trees (those with at least 75 % canopy loss and little chance of recovery) may reduce competition and light suppression, and theoretically improve the chances of the remaining trees. Thinning in this way is already implemented by some landowners and has been advised by other studies (Combes et al., 2024; Cracknell et al., 2023; Enderle et al., 2019).

Current management for large ash focuses largely on felling only hazardous individuals, preserving large/mature trees even if they are infected (Combes et al., 2024). We believe this practice is likely already the best course of action for large trees, as it maintains the carbon stocks and habitats they create for as long as possible. This aids in protecting the 953 species associated with ash (Mitchell et al., 2014) and will also preserve any resistant genetics that can increase the regeneration potential of UK ash populations.

Our results also highlight that carbon budgets and accounting frameworks (IPCC et al., 2006, 2019) should consider the carbon debt from infected trees that are compromised when calculating the contribution of forests in offsetting carbon emissions, to avoid over estimation of carbon stocks, sink capacity and mitigation effects.

5. Conclusions

Despite the high frequency of infections, we show that mortality of ash trees has not significantly changed since the introduction of ash dieback and that ash carbon stocks have continued to increase. These results suggest that the forests are in a lag phase, in which mature trees continue to survive despite being potentially fatally infected. Our results highlight the complexity of host-pathogen-environment interactions in forests, and the potential wider ecosystem impacts of tree population losses. Greater understanding of the many diseases faced by temperate tree species are required for creation of mitigation strategies and management practices that will allow for more accurate carbon stock estimates and accounting frameworks, while also ensuring benefits to all tree species and conservation of the forest as a whole.

CRediT authorship contribution statement

Rachel Mailes: Writing – review & editing, Writing – original draft, Visualisation, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualisation. **Bruno B. L. Cintra:** Writing – review & editing, Methodology, Data curation, Conceptualisation. **Rodrigo S. Bergamin:** Writing – review & editing, Data curation, Conceptualisation. **Laura J. Graham:** Writing – review & editing, Methodology, Supervision. **Estrella Luna:** Writing – review & editing. **Matthew S. Heard:** Writing – review & editing, Supervision. **Thomas J. Matthews:** Writing – review & editing, Supervision. **A. Robert MacKenzie:** Writing – review & editing. **Roel Brienen:** Writing – review & editing. **Adriane Esquivel-Muelbert:** Writing – review & editing, Supervision, Methodology, Conceptualisation, Visualisation, Investigation.

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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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123575.

Data availability

Data collected by the authors will be made available. The authors do not have permission to share the historical data.

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