



# Unravelling a hidden synergy: How pathogen-climate interactions transform habitat hydrology and affect tree growth

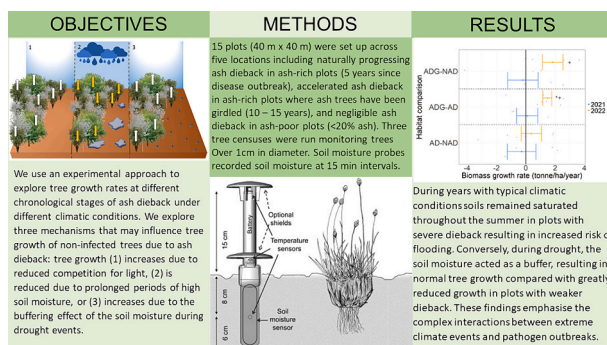
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## HIGHLIGHTS

- We show complex interactions between pathogens, climate, and tree growth.
- Tree dieback had a buffering effect on growth of remaining trees during drought.
- Weak tree dieback resulted in reduced tree growth during drought.
- During typical climatic conditions tree dieback increased soil moisture.
- Saturated soils due to tree dieback increase the risk of floods and runoffs.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Interactions between multiple global change stressors are a defining characteristic of the Anthropocene. Tree-associated pathogens are affecting forested ecosystems worldwide and occur in the context of increased frequency and intensity of extreme climate events such as heat waves, droughts, and floods. The effects of these events, along with subsequent changes in environmental conditions, on remaining and regenerating trees, are not well understood but crucial for the restoration and conservation of forested habitats.

In this study, we investigate ash (*Fraxinus excelsior*) dieback in a temperate broadleaf woodland as a case study to explore the processes influencing non-infected trees during pathogen-induced mortality events. Utilising an experimental setup, we examine tree growth rates at different chronological stages of the disease, including naturally progressing ash dieback (4–5 years since disease outbreak), accelerated ash dieback where ash trees have been girdled (10–15 years), and negligible ash dieback (<20% ash trees).

During a year with typical climatic conditions (2021), soils in accelerated ash dieback plots remained saturated throughout the summer due to insufficient transpiration (57% higher in the accelerated dieback plots), suggesting a significantly increased risk of summer run-off and floods. However, tree growth rates in these plots were not affected (*t*-test,  $t = -0.3$  to  $1.2$ ,  $p > 0.05$ ). Conversely, anomalously dry years, such as the 2022 summer drought, saw higher soil moisture in the accelerated ash dieback plots (*t*-test,  $t = 4.8$ ,  $p < 0.01$ ) acting as a buffer, resulting in normal tree growth during drought compared to greatly reduced growth in plots with weaker dieback.

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These findings emphasise the complex interactions between extreme climate events and pathogen outbreaks. Better understanding of the relationships between pathogens and hydrology on tree growth is imperative and detailed long-term studies on tree growth and hydrology will facilitate and improve mitigation strategies.

## 1. Introduction

The increased frequency of major tree pathogen outbreaks is a key feature of global change and is primarily rooted in increased global trade and connectivity, an underrecognised dimension of the Anthropocene (Malhi, 2017). Increased pathogen outbreaks are arguably the strongest aspect of global change in moist temperate forests, surpassing climate change, land use, and fire in its impacts of forest structure and function. Fungal pathogen outbreaks have increased in recent decades (Brasier, 2008; Fisher et al., 2012; Roy et al., 2014; Sikes et al., 2018) which is likely due to imperfect global biosecurity coupled with long-lived environmental stages, particularly of the phylum Ascomycota. Rising global temperatures are expected to expand the geographical range of pathogens which will increase the frequency of outbreaks further (Porta et al., 2008). In the U.S. it is estimated that 5.5 Tg carbon of live tree biomass is lost annually due to the 15 most dominant tree pathogens (eight of which are fungi) (Fei et al., 2019).

Following tree mortality events, there is often compensatory growth in surviving and uninfected trees (Anderegg et al., 2016; Wang et al., 2012); however, it can take several decades for the woody biomass to reach pre-mortality levels (Fei et al., 2019). Increased frequency of pathogen outbreaks therefore reduces the possibility of biomass recovery which will affect forest structure, recovery, and regeneration.

When tree mortality exceeds 20 %, reductions in evapotranspiration have been shown to affect habitat hydrology and soil water content (Anderegg et al., 2013). In most cases, habitat evapotranspiration is reduced following tree mortality events, which subsequently increases soil moisture; however, the opposite effect has also been observed. In drier regions, an increase in near-ground solar radiation and wind due to canopy loss increases habitat evapotranspiration and therefore reduces soil moisture following tree mortality (Adams et al., 2012; Biederman et al., 2014; Guardiola-Claramonte et al., 2011; Troendle et al., 2010). These hydrological effects normally assume tree mortality as the main cause of reduced transpiration, however, Frank et al. (2014) show that evapotranspiration is markedly reduced at the initial stages of pathogen infection with only a small reduction following tree death. This suggests that tree pathogens can have a near-instant effect on the habitats they inhabit by altering the hydrological dynamics of individual trees.

High soil water content has been shown to support plant growth (Anderegg et al., 2016) but if the soil is waterlogged, or the water content has been high for a prolonged period of time, it may cause increased mortality through induced stress that reduces photosynthesis and respiration, limits root activity and nutrient cycling, and disrupts metabolism (Pan et al., 2021). As well as inducing mortality, waterlogging reduces reproductive growth, germination and seedling establishment (Pan et al., 2021; Zhou et al., 2020) which are likely to impact on plant regeneration. Physiological adaptations may reduce mortality rates during prolonged floods (Pan et al., 2021; Zhou et al., 2020) and root associations with arbuscular mycorrhiza can support plants by providing oxygen and resources (Tuheteru and Wu, 2017). Tree species respond differently to waterlogging and in British woodlands oak (*Quercus robur*) and ash (*Fraxinus excelsior*) are relatively tolerant, while sycamore (*Acer pseudoplatanus*) and beech (*Fagus sylvatica*) are more sensitive (Kreuzwieser and Rennenberg, 2014).

Ash trees (*Fraxinus* spp.) are succumbing widely to dieback at a global scale. The emerald ash borer beetle (*Agrilus planipennis*) has devastated ash populations in North America since the early 2000s (Herms and McCullough, 2014), while the fungal pathogen *Hymenoscyphus fraxineus* has affected populations of ash trees in Europe since the early 1990s (Vasaitis and Enderle, 2017; Zhao et al., 2012). The

latter was first detected in Britain in 2012 following the importation of infected ash trees from the Netherlands (Potter and Urquhart, 2017); although some evidence suggest that the disease arrived even earlier (2004–2005) in England (Wylder et al., 2018). The European ash dieback is estimated to cause 70 % mortality with the highest proportion of mortality found in younger trees (Matisone and Matisons, 2021). This will have a major impact on ash regeneration (Vasaitis and Enderle, 2017) and long lasting effects on woodland ecology. In North America, mortality due to the emerald ash borer is nearer 100 % (McCullough et al., 2009) and mainly affects older trees as the bark beetle requires a certain tree size to complete its life cycle. The impacts of tree mass mortality events caused by species specific pathogens are complex and likely to permanently change ecosystems due to the long-term removal of specific species.

While the impacts of pathogens on the infected trees are widely studied (e.g. Díaz-Yáñez et al. (2020)), little is known about how remaining and regenerating trees respond to mass mortality events and the subsequent changes in environmental conditions. It is also unclear how trees will respond to changing climatic conditions and the interactions with pathogen outbreaks. In this study we use ash dieback in a British temperate broadleaf deciduous woodland as a case study to explore the processes that influence non-infected trees during pathogen induced mortality events (see Fig. S1 for a conceptual outline of the three main mechanisms influencing tree growth in the study region). We use an experimental set up to explore tree growth rates at different chronological stages of the disease including naturally progressing ash dieback at the early stages of the disease (5–6 years after pathogen arrival), accelerated ash dieback (girdled ash trees represent 10–15 years after pathogen arrival), and negligible ash dieback effect (mixed stands with <20 % ash trees). Specifically, we ask:

1. What is the impact of tree dieback on soil moisture and light availability?
2. How are the growth rates of non-infected trees altered by tree dieback?

## 2. Materials and methods

### 2.1. Study site

The study took place in Wytham Woods in southern Britain (51° 46' N, 001° 20' W) which are situated on a hill spanning an altitudinal range of approximately 100 m (56 m–166 m asl). The mean annual temperature and annual rainfall are 10 °C and 726 mm, respectively (Butt et al., 2009). The woods are dominated by tree species such as sycamore (*Acer pseudoplatanus*), common ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*), oak (*Quercus robur*), and hazel (*Corylus avellana*). Ash trees in an 18-ha plot in the centre of the woods represent 32.8 % of the individual trees and 20.1 % of the total basal area (m<sup>2</sup>/ha) (Butt et al., 2009, supported by more recent unpublished data). Ash dieback is therefore expected to have a major effect on the structure and ecology of the woodland. The disease was first detected in Wytham Woods in 2017 and by the end of the study in September 2022 the majority of ash trees in the experimental plots were showing signs of the disease.

### 2.2. Study design

The study was conducted in 15 plots (40 m × 40 m) nested within five clusters across the woods (Fig. S2). Each cluster contained three habitat types which were used to examine the difference between ash

and non-ash dominated habitats as well as the impact of simulated ash dieback through girdling.

- Ash dominated (AD): Habitat dominated by ash trees and characterised by high understory biomass of mainly sedges, grasses, and bramble. This habitat type represents naturally progressing ash dieback and during the study the disease had been present in the woods for 4–5 years.
- Ash dominated and girdled (ADG): Like the AD plots, the ADG plots, were dominated by ash trees with high understory biomass. In these plots all ash trees were girdled to reach the sapwood (approximately 3 cm depth) between December 2019 and February 2020 to accelerate the impacts of ash dieback and mimic a scenario where the disease has been present for 10–15 years.
- Non-ash dominated (NAD): Mixed species plots with a maximum of 20 % ash and a strong presence of sycamore, beech, oak, and hazel. This habitat type represents mixed species stands where ash dieback plays a smaller role. These plots are used to examine the differences between ash dominated and non-ash dominated habitats.

### 2.3. Data gathering

#### 2.3.1. Biomass estimates and tree growth rates

Tree censuses were conducted in each plot in November 2020, September 2021, and September 2022 during which all trees were identified to species and the diameter at breast height (DBH) was recorded at 1.3 m. All trees with a diameter above 1 cm were measured.

DBH measurements were converted to woody biomass following the steps below. First, tree volume was calculated using Eq. (1) (Bunce, 1968).

$$\ln(V) = a_1 + a_2 * \ln(DBH) \quad (1)$$

where  $V$  is volume in  $m^3$ ,  $a_1$  and  $a_2$  are species-specific allometric constants (Table S1), and  $DBH$  is diameter at breast height (1.3 m) in metres. The tree volume was then used to calculate tree biomass in Eq. (2).

$$B = V * WD \quad (2)$$

where  $B$  is biomass in kg and  $WD$  is species-specific wood density in  $kg/m^3$  (Table S1).

Individual tree biomass growth rates (hereafter referred to as tree growth rates) were calculated by subtracting the biomass stock in one year by that of the previous year. To examine tree growth rates among species and size class categories tree specific data were used. The water content in the bark impacts the measured DBH and so to counteract inflated positive growth, negative values were also allowed in the analysis (Sheil, 2003). Since the density of non-ash trees in ADG and AD was lower than the tree density in NAD, the data were standardised in order to examine growth rates at the plot level. The average tree growth rate per plot was multiplied by the overall tree density plot average (mean tree density per 0.16 ha plot = 140.2 trees, mean tree density per ha = 876.25 trees). The 2020/2021 season was only ten months due to the late start of the census in November 2020 which missed the tree growth in September and October. However, as growth rates slow during the latter months of the year in Britain, this had a negligible effect on the results. From here on the growth period November 2020–September 2021 is referred to as the growth year 2021, while the period September 2021–September 2022 is referred to as the growth year 2022.

#### 2.3.2. Air temperature and rainfall

Air temperature and rainfall representing the general climate at Wytham Woods were recorded by an Automated Weather Station (AWS) in a grassland habitat at 160 m (asl) adjacent to the woods (UK National Grid: SP46150820). Air temperature was recorded hourly at 1.3 m using a CR1000 datalogger and rainfall was recorded using a tipping bucket rain gauge (unpublished dataset, provided by Stefanie M. Schäfer and

Denise Pallett, UK Environmental Change Network (ECN) site at Wytham - meteorology data 2012–2022) (see Morecroft et al. (1998) for further details).

A five-year average was derived for both mean monthly temperature and total monthly rainfall, utilising data from the years 2012 to 2018. Subsequently, mean monthly air temperature and total monthly rainfall were computed for the study period November 2019 to November 2022. These datasets were employed to assess whether the study conditions exhibited anomalies relative to the long-term averages.

#### 2.3.3. Light availability and soil moisture

Light availability below the canopy (3 m height) was recorded in three cardinal directions (East, South, and West) in the centre of each plot at 10-minute intervals using a LUX sensor for photosynthetic active radiation. Light availability was averaged across the three sensors in each plot. To standardise the measurements, and account for seasonal and temporal variations, the light availability an hour either side of the solar noon was used to create an annual average for each plot.

Soil volumetric moisture was measured to a depth of 10 cm in five locations in each plot using TOMST data loggers (Wild et al., 2019). The soil moisture data were recorded at 15 min intervals. Soil moisture was averaged across the five data loggers to create plot means. Daily and then monthly soil moisture averages were established for each plot.

### 2.4. Statistical analysis

Statistical analyses were conducted in R (version 4.1.0) with associated packages. Data were visualised using [ggplot2] unless otherwise stated.

Tree annual growth rates above 10 cm were removed due to suspected measurement error. Mixed linear models [lmer] with plot as the random factor were used to examine the tree dieback effects on soil volumetric moisture and light availability over time. Model variance [MuMIn: r.squaredGLMM] and Akaike Information Criterion (AIC) were calculated to examine the fit of the model.  $t$ -Tests [t.test] were employed to compare the monthly differences in soil moisture across habitat types.

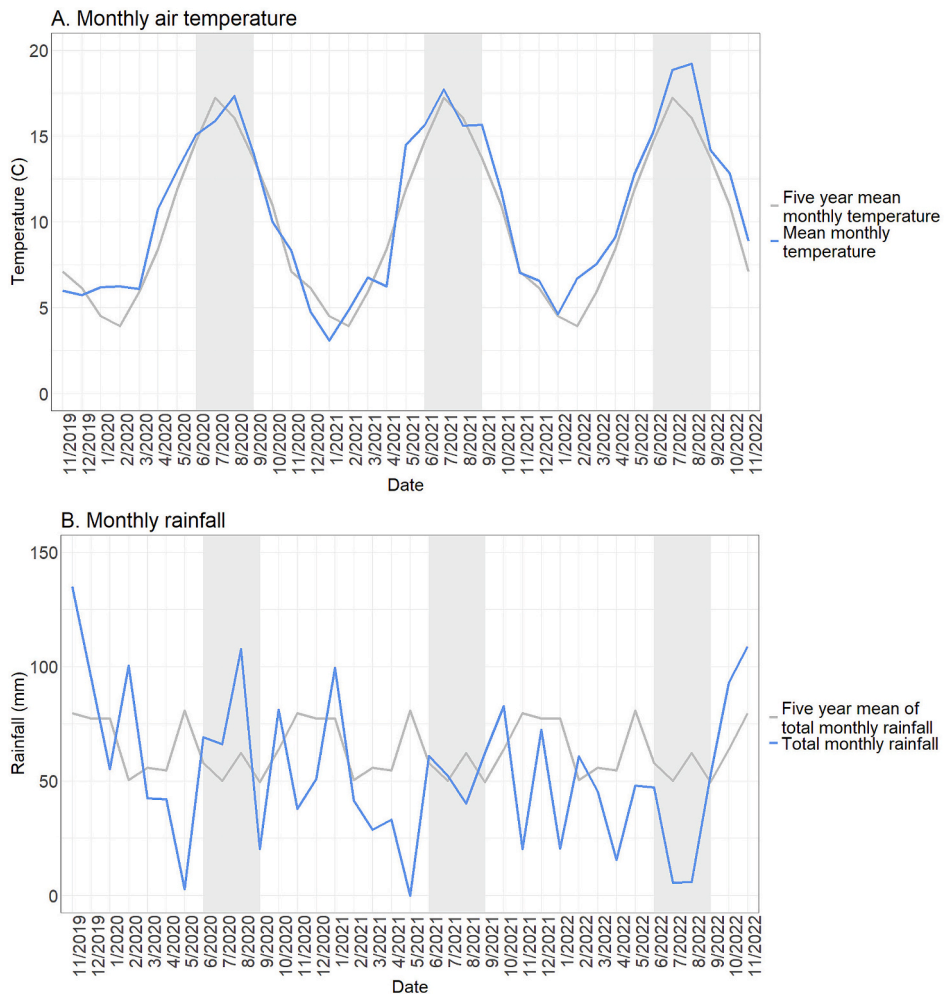
Individual annual tree growth was averaged at the plot level and a linear model [lm] was used to examine the association between tree growth, size class and species. Tree species that were represented by <15 individuals across the 15 plots were pooled and categorised as “other”.

The relationship between mean annual volumetric soil moisture and tree growth was explored using locally weighted scatterplot smoothing [stat\_summary(method = loess)], a non-parametric regression method ideal for capturing complex, nonlinear patterns in the data (Cleveland et al., 1991).

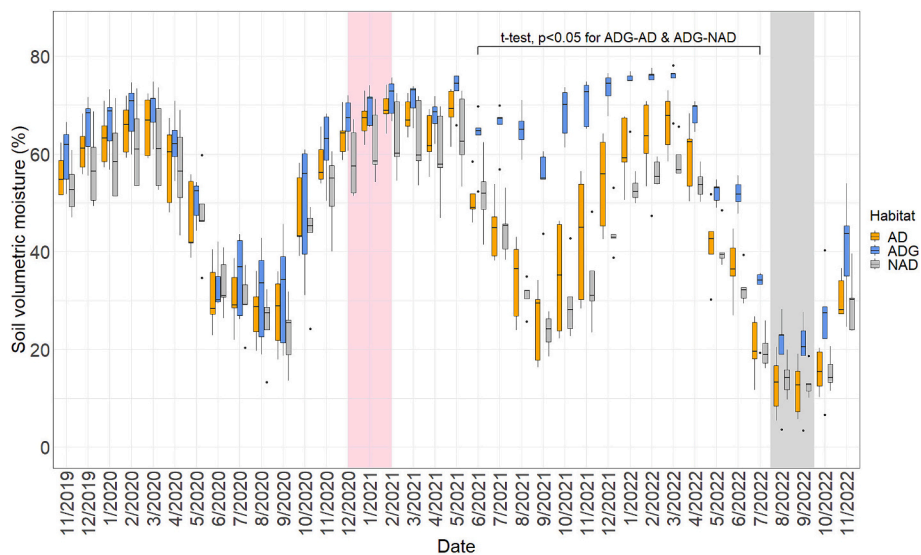
Tree growth differences between habitat types were calculated as the difference between paired habitats for each year (e.g. tree growth<sub>ADG,2021</sub> – tree growth<sub>AD,2021</sub>). This was done to examine how tree growth responded to the varying conditions in the different habitat types. To examine whether the delta was statistically different from zero, One-Sample  $t$ -tests [t.test] and Cohen’s D effect sizes [effectsize: cohens\_d] were calculated with zero as the independent variable.

## 3. Results

The air temperatures in 2020 and 2021 were similar to the five-year average, except for a milder winter in 2020, with very little discrepancy in the summer months (Fig. 1). However, July and August 2022 were 9.0 % (mean temperature = 18.9C) and 16.7 % (mean temperature = 19.2C) warmer than the five-year average, respectively. Rainfall patterns over the period 2020–2022 were variable and while 2020 and 2021 had relatively dry springs (April, May) the summer months (July, August) were wet or close to the five-year average. The year 2022 was generally dry compared with the five-year average with 89.0 % and 90.7 % less rain in July and August, respectively (Fig. 1). The dry



**Fig. 1.** Wytham Woods mean monthly air temperature (A) and total monthly rainfall (B) based on data generated using an Automated Weather Station (AWS) which is part of the Environmental Change Network (ECN). The trends are based on data between 2012 and 2022. The grey shadings represent the summer months (June, July, August). The grey line represents the five year mean of monthly temperature and total monthly rainfall between 2012 and 2018, while the blue line represents the observed monthly temperatures and total monthly rainfall during the study period 2020–2022.



**Fig. 2.** Soil volumetric moisture averaged at the plot level. Different coloured boxes indicate the different habitat types: ash dominated (AD), ash dominated and girdled (ADG), and non-ash dominated (NAD). The pink shaded area represents the period when girdling took place, and the grey shaded area is the drought period in 2022.

summer coupled with high temperatures in 2022 resulted in a period of drought.

In total, 2103 trees were censused in the 15 plots every year. Data from 147 trees were removed due to suspected measurement error and ash trees were excluded in order to examine the growth of non-ash trees due to the prevalence of the disease in the woods. This resulted in the analysis of 1415 trees between November 2020 and September 2022. In 2019 and 2020, prior to ash girdling, monthly average soil volumetric moisture did not vary among the different habitat types (Fig. 2). Following girdling there was a significant difference between the girdled plots (ADG) vs the ash dominated (AD) and non-ash dominated (NAD) plots (*t*-test,  $p < 0.05$ ) and during the period June 2021 – June 2022 soil moisture was up to 57 % higher in the ADG plots. However, after a period of low rainfall and above-average temperatures in July–August 2022, the difference between habitat types decreased to be non-significant (Fig. 2).

Mean annual tree growth was significantly associated with tree species (ANOVA,  $F = 3.3$ ,  $p < 0.01$ ) and size class (ANOVA,  $F = 22.2$ ,  $p < 0.001$ ). Hawthorn had the lowest tree growth ( $3.0 \pm 2.8$  kg/tree/year), while tree growth was highest in beech ( $21.8 \pm 5.0$  kg/tree/year) which was significantly higher than the mid-story species hazel, field maple and hawthorn (*t*-test,  $t = -3.1$  to  $-2.3$ ,  $p < 0.05$ ) (Fig. 3). Size classes also differed in tree growth with highest growth rates in the 50.1–60.0 cm category ( $33.9 \pm 3.7$  kg/tree/year) which was significantly higher than the other size categories (*t*-test,  $t = -3.3$  to  $4.9$ ,  $p < 0.05$ ) except for the category 40.1–50.0 cm ( $26.0 \pm 2.9$  kg/tree/year) and  $> 60.1$  ( $32.3 \pm 4.4$  kg/tree/year) (Fig. 3). The lowest rate of tree growth was recorded in the smallest size category 1.0–10.0 cm ( $0.9 \pm$

1.7 kg/tree/year) which was significantly different from all other size categories (*t*-test,  $t = 2.5$  to  $6.8$ ,  $p < 0.05$ ).

Tree growth at the hectare level had a quadratic relationship with average annual soil volumetric moisture (Table 1). The quadratic tendency in the data was supported by the general trend that was produced using a non-parametric regression (loess) (Fig. 4, see Fig. S3 and Table S2 for plot specific tree species demographics). The quadratic relationship explained 19.5 % of the variance in the data. Both drier and wetter conditions reduced tree growth to zero at 31 % and 77 % annual average soil moisture (Fig. 4).

Intra-year tree growth rate comparisons between paired habitat types showed that there was no significant difference between habitats in the 2021 growth period (*t*-test,  $t = -0.3$  to  $1.2$ ,  $p > 0.05$ ) (Fig. 5). In 2022, tree growth in the girdled plots (ADG) was significantly higher than in the AD plots (*t*-test,  $t = 4.8$ ,  $p < 0.01$ ). Modelled effect sizes were high when comparing ADG plots with AD (Cohen's  $D = 2.2$ ) and NAD plots (Cohen's  $D = 1.8$ ), while there was no difference between AD and NAD (Fig. 5).

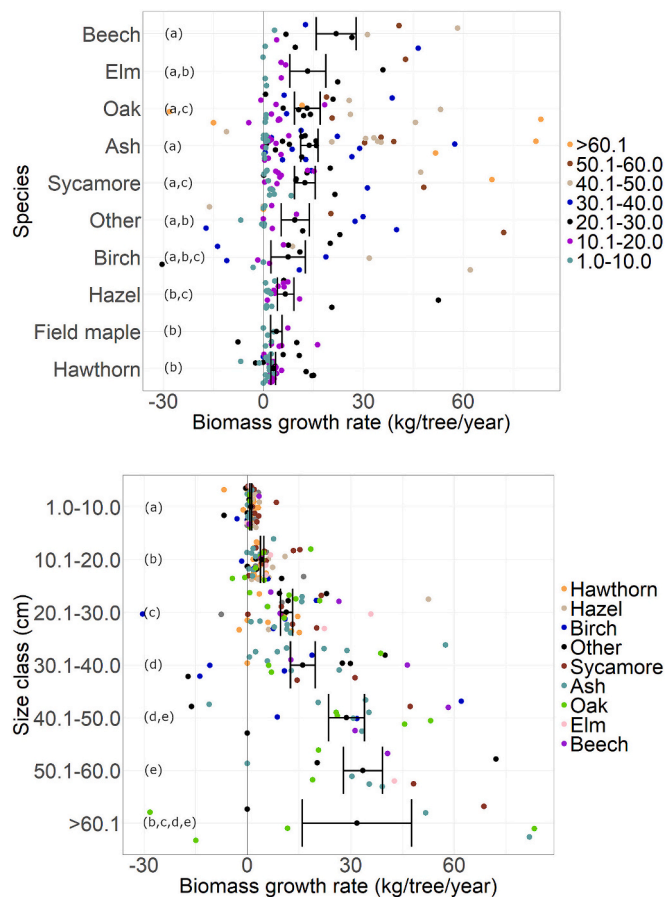
## 4. Discussion

### 4.1. Tree dieback and soil moisture

During tree mortality events, tree water uptake is reduced due to hydraulic failure and damages to the xylem (Anderegg et al., 2016; Oliva et al., 2014). Tree water transpiration is subsequently reduced which results in lower habitat evapotranspiration unless canopy loss increases surface evaporation due to increased heat or if rainfall is lower than 500 mm per year (Adams et al., 2012).

During the study, near-ground light availability did not change with either naturally progressing ash dieback or accelerated ash dieback. However, ash girdling had an almost instant effect on soil moisture.

Following ash girdling in the ADG plots at the end of 2020 the soil moisture stayed high over the summer 2021, while the soil dried in accordance with seasonal trends in the AD and NAD plots. The quick increase in soil moisture following ash girdling is likely to be due to the reduction in transpiration which has been shown to decline shortly after a pathogen outbreak (Frank et al., 2014), suggesting that pathogens can have a major effect on tree hydraulics at the early stages of infection. Moreover, the alteration in soil moisture dynamics resulting from ash dieback and girdling can have significant implications for flood risk assessment. High soil moisture levels, as observed following ash girdling in the ADG plots, can increase the risk of flooding due to reduced water infiltration capacity and enhanced surface runoff. This increased runoff can lead to elevated river flow levels and decreased soil water absorption during periods of intense rainfall, exacerbating the likelihood of flash floods and inundation in downstream areas (Baugh et al., 2020; Meng et al., 2017). The persistent elevation of soil moisture levels in the ADG plots highlights the potential for prolonged flood risk in areas affected by ash dieback. The soil moisture in the girdled plots (ADG) remained high for 14 months until the 2022 drought, when there was no



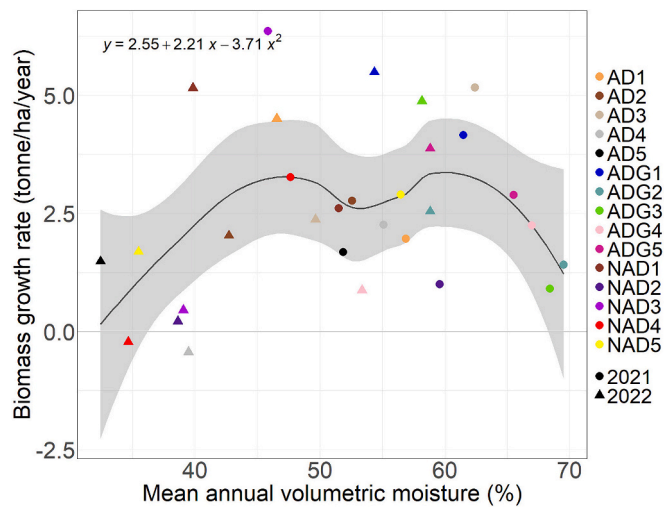
**Fig. 3.** Annual woody biomass accumulation per tree averaged at the plot level (kg/tree/year) for each species (A) and size class (B). Different letters indicate significant differences between groups. Each data point represents the average tree growth in each plot.

**Table 1**

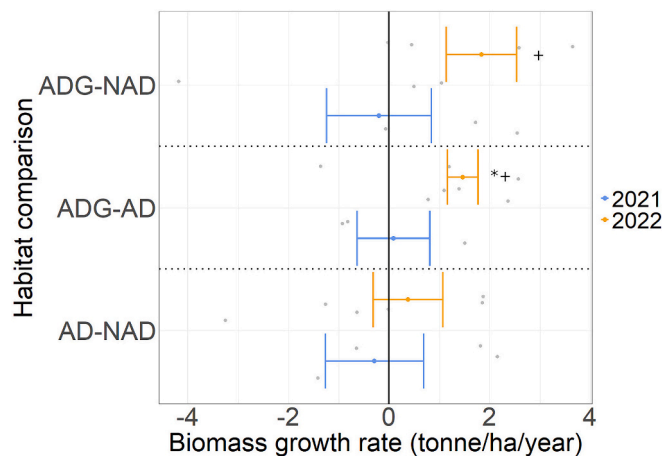
Full and minimal adequate linear mixed effects model with *tonne/ha/year* as the dependent variable.

Terms	numDF	F-value	P-value
Full model			
Soil moisture	1	4.8	<0.05*
Soil moisture <sup>2</sup>	1	4.2	0.05*
Light	1	0.07	1.0
Year	1	0.002	0.8
Minimal adequate model			
Soil moisture	1	5.8	<0.05*
Soil moisture <sup>2</sup>	1	5.2	<0.05*

\* Indicates significant *p*-values.



**Fig. 4.** Relationship between mean annual soil volumetric moisture (%) and woody biomass growth rate (tonne/ha/year). The quadratic equation describes the general relationship which is supported by the linear mixed model in Table 1. Different point shapes represent each of the 15 plots (ash dominated (AD), ash dominated girdled (ADG), and non-ash dominated (NAD)). The grey shaded area is the 95 % confidence interval. Blue points represent data from 2021 and orange points represent data from 2022. Each data point represents the average annual growth rate for individual plots.



**Fig. 5.** Difference in biomass growth rates (tonne/ha/year) between habitat types. Points and whiskers represent means and standard errors at the plot level among ash dominated (AD), ash dominated girdled (ADG), and non-ash dominated (NAD) plots. Blue whiskers represent data from 2021 and orange whiskers represent data from 2022. \* indicates significant differences from zero and + indicates large effect sizes (Cohen's  $D > 1$ ).

distinguishable difference in soil moisture among the habitat types. In November 2022 there were signs of more rapid recovery in soil moisture in ADG, suggesting that the soil moisture was starting to diverge again following the drought event.

In this study light availability, and by extension canopy cover, did not decline in either the ADG plots or in the AD plots suggesting that the differences between plots are based on a reduction in water transpiration and not evaporation off the surface. In 2022, the drought resulted in soil moisture levels becoming more uniform due to the widespread soil desiccation which subsequently reduced the statistical difference among habitat types. In regions with relatively low annual rainfall, such as Wytham Woods (700 mm), abnormally dry and hot years may swing the balance between rainfall and evapotranspiration resulting in a reduction in soil moisture following tree mortality events. Climate change may

therefore have a major impact on how habitat hydraulics respond to pathogen outbreaks and tree dieback.

#### 4.2. Species and size class effects on tree growth

Species and size classes were significantly associated with tree growth. Among the observed tree species, beech accumulated the most woody biomass which was statistically higher than the growth of the mid-story species, while hawthorn exhibited the lowest biomass accumulation. Generally smaller trees accumulated less biomass per year than larger trees (Stephenson et al., 2014). However, trees in the largest size category ( $>60.1$  cm) had the highest variation in biomass accumulation and only differed significantly from the smallest size category (1.0–10.0). Studies have found that in 10 % of European tree species growth rates slow down in the largest trees as they reach a certain size (Stephenson et al., 2014). Beech, for which tree growth was the highest, was represented mainly by trees in the larger size categories (30 cm–60 cm) with a small fraction represented by trees below 10 cm. Shrinkage was seen across all species and size classes and may have been represented by mature trees. Large trees and trees with gnarly bark tend to be hard to measure accurately suggesting that some shrinkage may be due to measurement error. Tree growth differences among species in this study were largely due to tree size linked to metabolic scaling as there was a clear division between the overstorey species and the mid-storey shrubby species.

Living non-girdled ash trees had the third highest biomass accumulation rate out of the trees in this study, following beech and elm, and with a similar accumulation rate to oak. Ash trees are fast growing (Kirby, 2020) and comparisons with unpublished data from the same woodland between 2010 and 2016 suggest that biomass accumulation rates were similar to the ones reported in this study. These similarities suggest that ash dieback had a negligible effect on the tree growth of living non-girdled ash trees during the study.

#### 4.3. Tree dieback and soil moisture effects on tree growth

Tree growth had a generally unimodal relationship with soil moisture (here modelled as a quadratic) which resulted in reduced tree growth in the wettest plots in 2021 and near zero growth in the driest conditions in 2022. While both drier and wetter conditions have negative effects on tree growth, the drought during 2022 affected growth more than the wet conditions in 2021. This may be due to the ADG plots not becoming wet enough for long enough to reduce tree growth to zero (highest soil moisture was 70 %, while the highest model x-intercept was 77 %). However, if the wet conditions in the ADG plots had persisted, it is likely that the prolonged above-average soil moisture would have had a more negative effect on tree growth over the two years. Sycamore, beech, and field maple have been shown to be sensitive to waterlogging with damage (leaf fall, necrosis, bark damage) being detected between two weeks and two months of the roots being submerged, while damage in oak and birch has been detected after three to four months (Kreuzwieser and Rennenberg, 2014). Root depth may influence the sensitivity to drought.

There was no significant difference in tree growth among plots in 2021. In 2022, the drier conditions had a negative effect on tree growth in NAD and AD, while the higher soil moisture in ADG buffered against the drought which resulted in significantly higher tree growth compared with the other habitat types. The average difference in tree growth was higher between ADG and NAD than between ADG and AD which may have been due to the slightly higher soil moisture in AD. In 2022, ash dieback had been present in the woods for at least five years and so the increase in soil moisture in AD is likely to be a response to the ash dieback induced reduction in tree water transpiration and overall evapotranspiration (Adams et al., 2012; Andregg et al., 2016).

Our results suggest complex interactions between pathogens, climate, and tree growth in forest ecosystems. Prolonged periods of wet

conditions may have a damaging effect on tree growth, however, here we found that tree growth had a more drastic response to the short drought in 2022 than 14 months of higher-than-average soil moisture. The buffering effect that the increased soil moisture provided in the ADG plots suggests that a reduction in habitat evapotranspiration during tree pathogen outbreaks may protect the remaining uninfected and regenerating trees from drought events. However, when rainfall is lower than habitat evapotranspiration, pathogen induced tree mortality is likely to lower soil moisture (Adams et al., 2012) resulting in reduced rates of tree growth. It is possible that an increase in the frequency and intensity of drought events may have a similar effect which would impact on the survival of remaining trees during mass mortality events.

Ash trees thrive in a wide range of conditions, except for prolonged waterlogging and low pH, and dominate sites that are largely unsuitable for species such as beech and oak (Dobrowolska et al., 2011). Recolonisation of ash dieback affected areas may therefore be slow and hampered by site specific conditions. Water stress, whether from drought or waterlogging, can substantially increase a tree's vulnerability to pathogens (Heinzelmann et al., 2019; Kubiak et al., 2017). However, while these stressors heighten susceptibility following mass mortality events, waterlogging may also reduce the presence of certain pathogens in the soil, such as *Armillaria* (Szewczyk et al., 2016). This suggests that although trees face greater pathogen risks under adverse conditions, specific environmental factors like high soil moisture can concurrently suppress certain pathogens, influencing the dynamics of forest recovery and its response to species mass mortality events.

## 5. Conclusions

Increases in international trade and a warming climate are increasing the frequency and range of tree pathogen outbreaks (Porta et al., 2008). As the frequency of tree mass mortality events increase it is important to understand how remaining and regenerating trees are affected by the resulting conditions. In this study we found that accelerated ash dieback through ash girdling significantly increased soil moisture and left soils saturated over the summer months. The short drought in July and August 2022 had a stronger impact on tree growth than longer and wetter periods in 2021. However, it is likely that tree growth would have been reduced had the wetter conditions persisted. Instead, the higher soil moisture in the ash girdled plots buffered against the drought which resulted in significantly higher tree growth than in the other plots.

Ash girdling in this study had a major effect on soil moisture while light availability was not significantly different. The effect on soil moisture is supported by Frank et al. (2014) who found that water transpiration declined at the early stages of pathogen infection suggesting that tree pathogens play a major role in tree hydraulics. This shows the importance of considering hydraulics during pathogen outbreaks as it may be used as a detection of mass mortality as well as having a major impact on tree dynamics.

Soil moisture can either increase or decrease with tree mortality events (Adams et al., 2012; Anderegg et al., 2016) which means that future scenarios can go one of two ways. If rainfall is higher than habitat evapotranspiration the increased soil moisture may buffer against drought but may increase the rate of runoff, risk of flooding, and potentially harm the remaining and regenerating trees due to water damage. The latter depends on how wet the soil is and the length of time the soils are waterlogged (Kreuzwieser and Rennenberg, 2014). If rainfall is lower than evapotranspiration, tree mass mortality events would reduce soil moisture and have a negative effect on tree growth. As extreme weather events such as drought and heavy rainfall are expected to increase, the understanding of the hydrological impact on tree growth dynamics is necessary to ensure suitable management interventions. Long term data on tree dynamics in pathogen affected regions can provide insights into the interactions between climate and pathogen outbreaks, as would higher resolution tree growth data.

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## CRediT authorship contribution statement

**Cecilia A.L. Dahlsjö:** Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.  
**Yadvinder Malhi:** Writing – review & editing, Funding acquisition.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Dr. Cecilia Dahlsjö and Prof Yadvinder Malhi reports financial support was provided by Natural Environment Research Council. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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