

Neighbours matter and the weak succumb: Ash dieback infection is more severe in ash trees with fewer conspecific neighbours and lower prior growth rate

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Neighbours matter and the weak succumb: ash dieback infection is more severe in ash trees with fewer conspecific neighbours and lower prior growth rate

5 ABSTRACT

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- The epidemiology and severity of ash dieback (ADB), the disease caused by the ascomycete
 fungus *Hymenoscyphus fraxineus*, has been linked to a variety of site conditions, however,
 there has been a lack of analysis at an individual-tree scale.
- 2. Symptoms of ADB were scored on ca. 400 trees of Fraxinus excelsior (ash) in permanent 10 sample plots during two successive years in a UK natural woodland reserve. Using 11 comprehensive plot records maintained since 1945, and detailed spatial records updated 12 since 1977, we assembled an array of potential explanatory variables, including site 13 environment factors, ash tree density, previous and present tree condition and near 14 neighbourhood summary statistics (NNSS), such as species mingling and size dominance. Their 15 impact on the severity of ADB of focal ash trees was tested with generalised linear mixed 16 effects models (GLMM). 17
- 3. The severity of ADB was much greater in the lower slope parts of the site with moister soils and least in a managed area subject to tree thinning in the previous 35 years. Severity of ADB had a negative association with focal ash tree prior relative growth rate over a period of a decade immediately before the disease was detected at the site. Greater ADB severity was also significantly associated with smaller diameter at breast height of ash trees. Additionally, ADB was significantly positively associated with a greater proportion of heterospecific trees amongst the six nearest neighbours of the focal tree.
- 4. Synthesis. The relationship of the severity of ADB disease with site environment, tree
 condition and neighbourhood is complex but nevertheless important in the progression of the

- disease. The findings suggest some silvicultural interventions, such as thinning to increase the
- vigour of retained ash trees, might reduce the impact of ADB.
- 29 Keywords: tree pathogen, tree disease, forest dynamics, ash dieback, chalara, prior growth rates,
- ³⁰ species mingling, size dominance, basal area of larger trees, tree diameter

32 **1. INTRODUCTION**

33

Ash dieback (ADB) disease, caused by the ascomycete fungus Hymenoscyphus fraxineus, has plagued 34 European woodlands for nearly three decades. It has spread rapidly from East to West across the 35 continent causing a major impact on ash populations and large areas of ash-dominated woodlands. In 36 Europe, ADB was first recognised in Poland in the early 1990s (Kowalski, 2006) and was positively 37 identified as arriving in Great Britain by 2012, since when it has infected populations of European ash 38 (Fraxinus excelsior) across most of the UK (British Ecological Society, 2012; Pautasso et al., 2013; 39 Stocks, Buggs & Lee, 2017). There have been many location- and country-specific reports of ADB-40 linked ash mortality from across Europe. However, predicting eventual mortality rates in mature ash 41 trees is difficult due to the slow progression of the disease. Therefore, Coker et al. (2019) carried out 42 a meta-analysis of published studies, together with a time-dependent model, to estimate longer-term 43 mortality, leading to a pan-European prediction (with wide confidence intervals) of approximately 60% 44 average cumulative mortality in natural woodland. However, plantation trials of young trees have 45 shown that only 1-5% of the populations are genetically tolerant of ADB (e.g. Kjær et al., 2012; Stocks 46 et al. 2017). Nevertheless, it is likely that ADB will have a lasting impact on the 953 animal and plant 47 species associated with F. excelsior (Mitchell et al., 2014). ADB is one of the most researched topics in 48 recent European woodland ecological literature, yet half of the studies involved laboratory-based 49 experiments rather than in situ observations (Bowler, 2019). At present there is no effective 50 silvicultural or other management response to slow the spread of the disease, once it has arrived in a 51 region (Skovsgaard et al., 2017). Therefore, the primary focus has been on the long-term strategy of 52 tree selection and breeding for resistance as the basis for restoration of ash populations (McKinney et 53 54 al., 2014).

The disease induces symptoms of leaf wilting, dieback of twigs in the crown, and necrotic lesions in young shoots, bark, and leaf petioles. The clearest visible symptoms are epicormic sprouting on the trunk and branches (Enderle et al., 2018). Ascospores develop in the apothecia of leaf rachises

after they fall during the autumn and winter, and the following spring and summer they are released 58 and dispersed by wind (Timmermann et al., 2011; Gross et al., 2014; Timmermann et al., 2017), leading 59 to new infections and continuation of the cycle (Nemesio-Gorriz et al., 2019). This suggests that 60 proximity to an infected tree will influence the probability and severity of infection. Inoculum density 61 decreases rapidly up to 50 m from infected trees (Chandelier et al. 2014; Grosdidier et al., 2018), 62 however it is estimated that the mean dispersal distance of ascospores is between 0.2 and 2.6 km, 63 depending on the scale and dispersal kernel (statistical distribution of distances) fitted (Grosdidier et 64 al., 2018). 65

The level of disease in the population of ash within a woodland is positively associated with 66 various site factors, including air humidity and temperature, topography, occurrence and dimensions 67 of watercourses, soil type and moisture (Klesse et al., 2021; Grosdidier et al., 2020; Chumanová et al., 68 2019; Erfmeier et al., 2019; Havrdová et al., 2017; Skovsgaard et al., 2017). Woodland structural and 69 compositional factors may have an influence on ADB, including local tree density, light levels and tree 70 species mixtures (Chumanová et al., 2019; Erfmeier et al., 2019). Furthermore, research has suggested 71 that individual tree metrics may be correlated with ADB. Larger diameter trees, for example, have 72 been found to display milder symptoms with a slower progression of ADB in the crown (Enderle, 73 Stenlid & Vasaitis, 2019; Skovsgaard et al., 2010; Lenz et al., 2016; Marçais et al., 2016; Queloz, 2016; 74 Havrdová et al., 2017). Previous studies also indicate that smaller and slower-growing trees are more 75 susceptible to ADB and have higher mortality rates than larger, faster-growing individuals (Klesse et 76 al., 2021; Klesse et al., 2020; Enderle, Stenlid & Vasaitis, 2019; Enderle et al., 2018; Marçais et al., 77 2017). 78

Recent research on the landscape epidemiology of ADB in northern France concluded that *F. excelsior* trees in isolated agricultural settings were less affected by the disease than those within forests (Grosdidier et al., 2020). This can be attributed to differences in microclimate, with higher crown temperatures in isolated trees that may restrict pathogen development, and/or to lower host density (as found in a grassland biodiversity experiment by Mitchell et al., 2002). A previous large-

scale study of ash forests in the Czech Republic also suggested that higher tree density and the 84 proximity of certain tree species (such as *Quercus robur* and *Fagus sylvatica*), together with proximity 85 to the nearest ash stand, as well as physical site environmental factors, can worsen the impact of the 86 disease (Havrdová et al., 2016; Havrdová et al., 2017). Similarly, a nationwide study in Switzerland 87 found higher mortality probability in stands with humid microclimate and high abundance of ash 88 (Klesse et al., 2021). Thus, as well as the severity of ADB being linked to forest microclimate, proximity 89 and density of infected ash hosts has a major influence on the rate of spore arrival on a susceptible 90 tree. 91

The present study sought to determine the impact of a range of site environment, previous and present tree condition and near neighbourhood factors on the severity of ADB in a population of *F. excelsior* trees. The specific questions were: (1) is the severity of ADB greater with increasing tree density in the immediate neighbourhood of the focal tree; (2) is the severity of ADB less in trees that had a greater prior growth rate; (3) is the severity of ADB less in trees that had a greater crown dominance over their immediate neighbourhood; (4) is the severity of ADB less in trees whose neighbourhood is more dominated by heterospecific trees?

To answer these questions, we carried out a study during the early-mid stages of a developing ADB epidemic at Lady Park Wood, Monmouthshire, Wales, which has a well-established ash population in near natural growing conditions – most of the woodland has been left unmanaged for more than 70 years – as well as records of individual trees in permanent sample plots since 1945.

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107 **2.MATERIALS AND METHODS**

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109 2.1 STUDY SITE

The study site, Lady Park Wood, is a 36-hectare ancient woodland nature reserve containing 33 native 110 tree and shrub species, dominated by Tilia platyphyllos, Tilia cordata, Fagus sylvatica, Fraxinus 111 excelsior, Betula spp., Quercus petraea, Ulmus glabra and Taxus baccata. The soil across the woodland 112 is heterogenous; its span of pH is one of the widest ranges in a single British woodland – from 7.9 to 113 3.8 (Peterken & Mountford, 2017) despite limestone being the dominant bedrock. Soil pH was 114 measured in 288 samples over 72 evenly-distributed 200 m² plots (Peterken & Mountford, 2017), 115 which we subsequently mapped onto the tree sample sub-plots described below. GPS altitude 116 readings were taken in each sub-plot and used to calculate its mean slope gradient angle. 117

The long history of monitoring at the site provides rare longitudinal records from repeated censuses of all trees in ten long thin permanent sample plots, termed "transects". All are 19.8 m wide and oriented parallel with the slope, but they vary in length from 150 m to 500 m (Figure 1). The transects have historically been categorised and sub-divided depending on when there was last human-caused disturbance, e.g. coppicing or thinning, and also by topographic position or dominant soil type. In Figure 1 and Table 1 we have sought to clarify the classification of these zones within the site, which define the non-overlapping "stand types" analysed in this study.

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FIGURE 1. Map of Lady Park Wood, Monmouthshire, Wales, with the geographical location shown in the inset map. Stands in the unshaded areas ("young growth") were felled in 1942-3, leaving a shelterwood of larger individuals; the shaded areas ("old growth") were last coppiced ca. 150 years ago. Transects VII, VIII and IX occupy a separate topographic position with outcropping limestone and steep slopes: the "below cliff" stand, which is ecologically distinctive as the ground is much steeper, some felling took place in the early 1940s, and the relative density of *F. excelsior* and *Ulmus glabra* is higher than in the other stands. Transects I-VI were laid out and first recorded in 1944, VII-IX in 1955, and X in 1984. The majority of transect X is in stands thinned in 1984 and 1994, the "managed compartment", but there is some old growth at the cliff end and a small section of young growth at the top of the slope. The "colluvial fan" in the northern section of the wood is sampled by the lower two-thirds of Transect VI. Also shown are topographical zones, which differ in soil type and slope gradient, such as 'mid slopes', 'lower steep slopes' and 'upper plateau'.

TABLE I. Distribution of the number of 30.5-m (100-ft) length transect sections amongst topographic and management history stand types in each of the ten transects. Each section has an area of 604 m². There is no overlap between the stand types

Transect	Old growth (OG)	Young growth (YG)	Colluvial fan (CF)	Below cliff (BC)	Managed compartment (MC)	Total number
I	5	5	-	-	-	10
II	5	2	-	-	-	7
III	2	5	-	-	-	7
IV	3	7	-	-	-	10
V	4	7	-	-	-	
VI	-	2	4	-	-	6
VII	-	-	-	3	-	3
VIII	-	-	-	4	-	4
IX	-	-	-	3	-	3
Х	2	-	-	I	12	15
Total number	21	28	4	11	12	76
Total area (m ²)	12,680	16,910	2,420	6,640	7,250	45,900

Nine of the transects (I-IX) are in woodland unmanaged for 78 years, which has been enclosed 144 by a two-metre-high deer fence since 2007. There is considerable variation amongst and within them 145 in both topographic position and past management. Above the limestone cliff that bisects the 146 woodland into upper and lower sections, transects I-V each sample both "old growth" and "young 147 growth" stands (Figure 1). The former was last coppiced in 1870 and the latter in 1942 just before the 148 site became a reserve. Transect VI predominantly samples "young growth" woodland on well-drained 149 soils of what is known as the "colluvial fan". Transects VII-IX are shorter being confined to the 150 woodland below the limestone cliff. These "below cliff" stands are ecologically distinct being on 151 steeply sloping ground and affected by some felling of *Tilia* spp. in 1942 for aircraft production; they 152 have a higher relative density of F. excelsior and Ulmus glabra than in the other stands. Transect X was 153 added in 1984 in an adjacent "managed" unfenced compartment, the majority of which has been 154 thinned twice since then. Metrics of each stand type are given in Table 4. 155

Hand-drawn maps of the locations of the centre of each individual woody plant ≥1.3 m height 156 in transects I-VI were recorded on a Cartesian coordinate grid by reference to transect edge markers 157 with a regular 30.5-m spacing in 1977. Transects VII-X were similarly mapped in 1984-85. These 158 records were updated and checked for accuracy at each successive enumeration of each transect, 159 including in 2013 before ADB was first observed in the woodland and in anticipation of its arrival. For 160 the present study these maps were scanned digitally using Esri ArcGIS Pro[®] 2.7.3 (2021) software onto 161 Ordnance Survey digital maps and allocated their British National Grid coordinate values. The 162 geographical location of the centre of each tree was normalised for slope. After the initial enumeration 163 of each transect, all woody plants \geq 1.3 m height (with no minimum diameter limit) in transects I-IX 164 165 were identified to species, recorded as live or dead and measured for diameter at breast height (1.3 m, dbh) in 1955, 1977 and 1983, and in all ten transects in 1986, 1992, 2000, 2002, 2010, 2013 and 166 2018. In the case of the many multiple-stemmed coppice stools, an equivalent single diameter was 167 assigned, calculated from the sum of their stem cross-sectional areas. 168

170 **2.2 TREE ATTRIBUTES**

A total of 464 *F. excelsior* trees across the ten permanent transects, representing all live individuals ≥ 1.3 m height at the start of the study in 2019, were assessed for ADB symptoms in July and August 2019, and 381 during August 2020. The lower number in the second year is due to the increased restriction on field-work due to risk assessment and restriction of available time under that constraint. Therefore, our main statistical models were only applied to the more complete data set recorded in 2019. We have used the 2020 data solely to assess the overall rate of progression of the disease at the time of the study.

The severity of crown dieback was scored between 0 and 100% based on a visual estimation 178 of proportionate level of defoliation, similar to the assessment methods used in other studies of ADB 179 (Turczanksi, 2020; Grosdidier et al., 2020; Lenz et al., 2012). Two observers surveyed each focal tree 180 according to an agreed scale of crown defoliation in scoring classes of 0-10%, 10-20%, 20-30%, 30-181 40%, 40-50%, 50-60%, 60-70%, 70-80%, 80-90%, 90-100%, with their assessments calibrated at 182 regular intervals against photographs of previously agreed percentage defoliation scores to ensure 183 scoring did not drift over the study. Independent scoring of the same tree by each of the observers 184 was conducted periodically to guard against observer bias and the scoring of the transects was 185 carried out in random order to avoid confounding with topographic/stand type. Ash trees with a 186 score of 0% crown dieback and no trunk sprouting or other visible sign of infection were classified as 187 uninfected. 188

Annual mortality rate (AMR) of ash, as a simple indicator of change from before to after the onset of ADB in the study woodland, was calculated using the formula of Sheil et al. (1995): AMR = 1 $-(N_1/N_0)^{1/t}$, where N is the number of trees alive at each census and t is the number of years between census 0 and census 1. Two periods of recorded prior growth rates were selected: 1977 to 2013, and 2000-2002 to 2013. Basal area of each tree was also calculated from the dbh measurements as an explanatory variable in its own right for focal ash trees, but also to calculate

further explanatory variables, such as the total basal area of the stand. Basal area of larger trees 195 (bal), an indicator of the level of competition for light on the focal tree at the stand level 196 (Pommerening & Grabarnik, 2019; Wykoff, 1990), was calculated as the total basal area of all trees 197 larger or equal to the basal area of the focal tree *i* in the same sub-plot at a particular time *t* (Table 2, 198 formula 5). By "sub-plot" here we mean the regular subdivisions of the transect plots permanently 199 marked by stakes at 400-ft (121.9-m) intervals down the slope, which were used for ease and 200 accuracy of the successive enumerations of the transects but were also, it transpired during our 201 study, the most ecologically appropriate for near-neighbour spatial analysis. The size of each sub-202 plot of the transects was 19.8 m x 121.9 m (2414 m²) and they were arranged so that each lay 203 entirely within either the "old growth" or "young growth" stands". An alternative measure of a focal 204 tree's crown dominance relative to its neighbours was provided by the recording, in previous 205 enumerations, of each tree's crown position in four categories: ground, understorey, sub-canopy, 206 and canopy. 207

208

209 2.3 SPATIAL ANALYSIS

Spatial point-process methods were used to compute the Euclidean distances between nearestneighbour points within each 2414 m² sub-plot (as illustrated in Figure 2). The 'spatstat' package in R was used to estimate near neighbour summary statistics (NNSS). Using 'spatstat', a number of established individual-tree neighbourhood indices were calculated (Baddeley, Rubak & Turner, 2015; Illian et al., 2008; Pommerening & Grabarnik, 2019) for use as explanatory variables, as outlined below. We used the minus-sampling "NN1" nearest neighbour edge-correction method outlined by Pommerening & Grabarnik (2019), in turn based on Hanisch (1984), for all these NNSS.

217

(i) Species mingling (mi) and weighted species mingling (wmi)

Both species mingling (mi) and richness-weighted species mingling (wmi) are spatially-explicit

diversity indices. Species mingling (mi) is a calculated value between zero and one representing the

proportion of heterospecific (rather than conspecific) trees in the near neighbourhood of the focal 221 tree (Table 2, formula 1). So, if there are four neighbours counted and three are heterospecific, the 222 focal tree is given a species mingling value of 0.75. The total number of nearest neighbours (k) can 223 be varied according to the ecological context. We used a version of the formula which incorporates 224 weighting by the number of species in the k nearest neighbours, known as "richness-weighted 225 species mingling" (wmi) (Hui et al., 2011), with the weighting effect limited by the number of species 226 present in the focal tree's sub-plot (which sets the maximum possible number of species in k + 1227 trees at that location) (Wang et al. 2021) (Table 2, formula 2). The wmi index is thus a more 228 sophisticated version of the mingling index, which encompasses the component of species richness 229 in a tree's heterospecific near neighbourhood, producing a greater variation in index values between 230 trees. However, to test the use of wmi for assessing the dominance of ash trees' neighbourhoods by 231 heterospecific trees, we examined the linear correlation of wmi with mi for the 464 ash trees 232 included in the study; the Pearson correlation co-efficient (r) was 0.89 giving us full confidence in 233 selecting wmi for this purpose. 234

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236 *(ii) Size dominance (ui)*

The size dominance index (ui) measures the size of a focal tree relative to its *k* nearest neighbours (Table 2, formula 3). We used stem diameter (dbh) to describe size, but other size characteristics are also possible. The calculation of this index is similar to that of the species mingling index, with a value between zero and one, and the potential to vary *k* (Hui et al., 1998; Aguirre et al., 2003; Pommerening & Grabarnik, 2019).

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243 (iii) Local tree density (λ)

Local tree density around a focal tree (λ) was calculated using a kernel smoothing function in R (Baddeley, Rubak & Turner, 2015). It was originated by Diggle (1985) as "a method for estimating the



FIGURE 2. Locations and species of all trees in two transect sub-plots (19.8 m \times 121.9 m) generated using the 'spatstat' R package showing the prevalence of ADB. A. is an example of one of the "old growth" sub-plots in transect 1. B. is one of the "young growth" sub-plots in transect 3. The red dots are infected *F. excelsior* trees, with their size representing the severity of infection. Asymptomatic *F. excelsior* trees are shown as open circles. The data illustrated in these spatial plots were used to calculate species mingling, size dominance and tree density

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Sorbus torminalis

Cornus sanguinea

Malus sylvestris

Rosa spp.

Sorbus aria

Euonymus europaeus

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TABLE 2. Key formulae used to calculate the indices. k in all equations relates to the total number of nearest 253

254 neighbour trees considered in the formulae

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Equation	Variable name	Variable category	Formula NNSS definition		
Near neigh	bourhood summary statis	tics (NNSS) f	ormulae		
(1)	Species mingling (Gadow, 1993)	Species	$M_i = \frac{1}{k} \sum_{j=1}^{k} 1(species_i \neq species_j)$	$M_i \in [0,1]$	
(2)	Weighted species mingling (Hui et al., 2011; Wang et al., 2021)	Species	$M'_{i} = \frac{1}{k \cdot c} \sum_{j=1}^{k} 1(species_{i} \neq species_{j}) \cdot s_{i}$	S_i is species richness among k nearest neighbours of an including tree i; $c =$ min(S, $k + 1$), where S is total species richness of forest stand	
(3)	Size dominance (Hui et al., 1998; Aguirre et al., 2003)	Size	$U_i = \frac{1}{k} \sum_{j=1}^k 1(m_i > m_j)$	$U_i \in [0, 1]$	
(4)	Local density (Diggle, 1985; Baddeley, Rubak & Turner 2015)	Density	$\hat{\lambda}_t(x) = \left\{ \sum_{i=1}^n \delta_t \left(x - x_i \right) \right\} / p_t(x)$	$\hat{\lambda}_{t}$ = local intensity of focal trees $x_{i}, \delta(x)$ = kernel function, and $p_{t}(x)$ = end correction	
Focal tree	attributes formulae				
(5)	Basal area of trees > focal tree (Wykoff 1990; Pommerening & Grabarnik, 2019)	Size	$BAL_{i}(t) = G(t) \cdot (1 - p_{i}(t))$ with $p_{i}(t) = \frac{1}{G(t)} \sum_{\leq g_{i}(t)} g_{i}(t)$	Where <i>i</i> is a given tree at time <i>t</i> , basal area percentile is $p_i(t)$ of tree i denoting relative dominance, where $G(t)$ is basal area ha ⁻¹ of forest stand at time <i>t</i> .	
(6)	Basal area of tree (Gadow et al., 2021)	Size	$BA = \frac{\pi}{4} \cdot \sum_{i=1}^{n} dbh_i^2 \text{ in } \text{cm}^2$ $BA = \frac{\pi}{40000} \cdot \sum_{i=1}^{n} dbh_i^2 \text{ in } \text{m}^2$	<i>dbh</i> is diameter at breast height or 1.3 m.	
Stand attrib	butes formulae				
(7)	Basal area of forest stand (Pommerening & Grabarnik, 2019)	Size	$G = \frac{\sum_{i=1}^{n} g_i}{A}$	g_i is basal area of tree <i>i</i> in m ² , <i>N</i> is number of trees in stand, <i>A</i> is area of sample plot in ha	

256

& Grabarnik, 2019)

sample plot in ha

257 2.4 STATISTICAL ANALYSIS

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The complex dataset of Lady Park Wood is derived from a range of historical and primary sources, as 259 described above, which do not always overlap precisely and as such cannot be coerced into a single 260 overarching statistical model. We have therefore categorised the potential predictor variables into 261 two groups, which we have termed as 'non-spatial', dominated by edaphic and context-related 262 variables, and by spatially explicit point-process statistical characteristics (Table 3). Variables that exist 263 in both categories did not require post-processing in that they remain true to their original sources 264 and coincidentally provide a useful bridge between the two groups. The historical sampling strategy 265 was based on dividing the site into several different stand types and topographical zones. Our 266 statistical methods were selected knowing that the sampling and methods had all the hallmarks of 267 being nested and hierarchical (Wang et al., 2019). We used a model averaging approach (Dormann et 268 al. 2018). 269

Prior to the modelling we investigated the most plausible distribution of our response variable 270 (adb19) using the 'fitdistrplus' package, identifying a beta distribution as the most appropriate family 271 for the models (Supporting Information; Zuur et al., 2009; Delignette-Muller et al., 2015). For selection 272 of the predictor variables to include in the models, we assessed likelihood of collinearity amongst our 273 full set of variables using Pearson's correlation. Where variable pairs were strongly correlated 274 variables (> 0.7), only one was retained. We then identified variables that could not logically co-occur 275 as predictors (due to legacy methods and/or variables being derivatives of each other). An example of 276 inappropriate or at the very least uninterpretable inference might result from modelling of species 277 mingling at more than one of 4, 5 and 6 nearest-neighbour tree ranges. Where pairs could not be 278 279 precluded due to collinearity, a selection criterion for one of these pairs was applied using the lowest Akaike information criterion (adjusted for small sample size AICc) using the 'AICcmodavg' package 280 (Mazerolle & Mazerolle, 2017). This process reduced the possible predictor variables in the non-spatial 281

set to seven, with 128 model permutations, and in the spatial set to six variables, with 64 model
 permutations.

For the model averaging stage of our procedure, we started with an initial 'global model' for 284 each of the non-spatial and spatial models (formulae shown in the Supplementary Information). We 285 used sampling 'transect' number (1-10) as a random effect and visually checked residuals for 286 performance and comparison against the null model (Zuur et al., 2009). From the 128 non-spatial and 287 64 spatial model permutations we retained what are often defined as the 'top models' for each using 288 the 'MuMIn' package (Bartoń, 2022) based on delta AICc < 2, as scores between 0 and 2 can be broadly 289 considered equivalent despite potentially different combinations of predictors (Wagenmakers & 290 Farrell, 2004; Burnham et al., 2011). All seven predictor variables were present in the non-spatial top 291 models but one (ui6) was absent from the spatial top models (retaining the other five). These sets 292 were then averaged and explored. To assess the effect of selecting the weighted mingling index (wmi) 293 rather than the basic species mingling index (mi) a sensitivity analysis was carried out of the effect on 294 the top models of switching from wmi to mi. All the statistical analyses were conducted in the R 295 programming language and R Studio (R Core Team, 2021). A full description of the procedures for 296 selection of beta distribution, variable elimination, model selection and the top models are shown in 297 the Supplementary Information. 298

TABLE 3. List of response and predictor variables obtained from Lady Park Wood showing their potential for inclusion in non-spatial and spatial models. Log relative growth rate – short time period (rgr-s) data are not available for the managed compartment only due to lack of site access during 2000-2002. Formal definitions of the point process statistics are provided in Table 2

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	Description	Non-spatial model	Spatial model
Epidemiological (response) variable adb19	Disease score in 2019 (% converted to 0-1 scale for beta distribution)		•
Site / edaphic /focal tree attribute predictors			
stand type	Old growth (OG), young growth (YG), below cliff (BC), colluvial fan (CF), managed compartment (MC) with thinned sub-compartments MCI and MC2	•	•
transect	Transect number	•	•
pН	Soil pH	•	
gradient	Slope gradient (degrees)	•	
ash density	Density of F. excelsior trees in the sub-plot	•	
dbh77	Focal tree 1977 diameter at breast height (cm)	•	
dbh02	Focal tree 2000-2 diameter at breast height (cm)	•	

	dbh I 3 can I 9	Focal tree 2013 diameter at breast height (cm)•Focal tree canopy score in 2019•	•
	rgr-l rgr-s	Focal tree log relative growth rate – long time period (1977 to 2013)•Focal tree log relative growth rate – short time period (2000-2002 to 2013)•	
	Point process statistics predictors		
	wmi4 wmi5 wmi6 ui4 ui5	Weighted species mingling (k=4) Weighted species mingling (k=5) Weighted species mingling (k=6) Size dominance index (k=4) Size dominance (k=5) Size dominance (k=6)	• • •
	ba bal	Basal area of larger trees in sub-plot	•
	lambda	Local tree density	•
305			
306			
307			
308	3. RESULTS		
309			
310	3.1 SUMMARY STAT	ISTICS	
311	The annual rate	e of mortality (AMR) of ash trees increased greatly since ADB was first re	corded
312	in the woodland in 2013	3. In the young-growth stands, from an initial population of 376, AMR wa	as 0.1%
313	during 1992-2013 and 2	1.4% (of 368 trees) during 2013-2019, and in the old-growth stands AN	√R was
314	0.4% (of 107 trees) and	I 1.8% (of 98 trees) in the two periods, respectively. All other stand typ	es also
315	showed a marked incre	ase in AMR since 2013.	

317 **TABLE 4.** Tree attributes by stand type in Lady Park Wood in 2019, including absolute values for trees of all

318 species and all ash trees, relative values for ash and severity of ADB

Stand type	All trees density (trees ha ⁻¹)	Ash tree density (trees ha ⁻¹)	Ash tree relative density (% per plot)	All trees basal area (m² ha ⁻¹)	Ash basal area (m² ha⁻¹)	Ash relative basal area (% per plot)	All trees dbh (mean cm)	Ash dbh (mean cm)	% Ash infected in 2019	Mean ADB severity in 2019 (%)
Old growth	611	92	15%	37.2	8.3	22.4%	20.1	30.3	87%	40%
Young growth	1,343	236	18%	28.4	10.6	23.0%	10.9	13.9	85%	47%
Colluvial fan	1,258	100	8%	19.1	6.6	34.5%	8.4	22.6	95%	74%
Below cliff	616	70	11%	24.0	7.9	32.7%	14.7	29.3	89%	71%
Managed compartm ent	1,365	190	14%	19.3	6.8	14.3%	16.2	18.7	60%	25%
Mean	1039	138	13%	25.6	8.0	25.4%	14.1	23.0	83%	51%

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Across the woodland the proportion of all recorded ash trees that were infected with ADB by 2019 320 was 81% (the mean of the values per stand type was 83%, Table 4). This had increased to 95% by 2020. 321 There was also a marked increase in the proportion of recorded ash trees with > 80% crown dieback 322 from 24.5% in 2019 to 41% in 2020. Ash trees that had a below-canopy crown position in 2013 had a 323 markedly higher severity of ADB in 2019 and to a lesser extent in 2020 than those with a canopy or 324 sub-canopy crown position (Figure 3). The proportion of ash trees infected and the severity of ADB 325 were greatest in the stands on the colluvial fan and below the cliff, which are adjacent to a wide river 326 (Figure 1) and have moister soils (Peterken & Mountford, 2017) and where ash accounts for the 327 highest proportion of the total basal area (Table 4). In contrast, both the proportion of infected ash 328 trees and severity of infection were notably lower in the managed compartment (in which ash 329 accounts for the lowest proportion of the total basal area and where there has been recent thinning 330 of trees) than in all the unmanaged compartments (Table 4). However, no consistent associations were 331 found, at the whole stand level, between the incidence of ADB infection and tree density (of all species 332 and of the absolute and relative density of ash specifically). 333



FIGURE 3. Severity of ADB (level of crown defoliation of ash trees): (a) across the whole woodland in 2019 and 2020 shown as frequency of the number of trees scored in each 10% class of defoliation; (b) box-and-whisker plot of ADB severity in the section of the forest with the greatest density of ash trees, the young growth stands, for trees with each of four crown positions in 2019 and (c) 2020. Trees with crowns in the canopy and sub-canopy are clearly less affected than those in the understorey and near the ground. Dieback severity increased in canopy and sub-canopy trees between 2019 and 2020

337 3.2 NON-SPATIAL MODELLING

Results from the model selection procedure are provided in full in the Supporting 338 Information. The resulting models for the prediction of ADB in 2019 by the non-spatial 339 predictors outlined in Tables 2 and 3 included stand type and six other variables that made 340 an independent contribution to the variation between trees in their severity of ADB (Figure 341 4, Table 5). There is strong evidence that greater ADB severity was associated with smaller 342 2013 diameter at breast height, lower relative growth rate (between 2000-2002 and 2013) 343 and lower soil pH. The severity of ADB was much less in the young growth and old growth 344 stand types than the below cliff and colluvial fan stand types. It was only very weakly 345 associated with longer-term past relative growth rate, density of ash trees in the same sub-346 plot or slope gradient. 347





FIGURE 4. Non-spatial model a) Effect (model average coefficient) of non-spatial predictors on adb19 severity. Single
 effect plots of the association of adb19 severity with each retained variable: b) stand type, c) pH, d) gradient, e) ash density,
 f) dbh13, g) rgr-s and h) rgr-l. Variable abbreviations are defined in Table 3. All panels include 95% confidence intervals
 coloured red or green for negative or positive average effects respectively

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TABLE 5. Non-spatial variables predicting the severity of ash dieback in 2019. Estimated regression parameters,

standard errors (SE), z-values, p-values and confidence intervals (CI) for model averaging and composite GLMMs

of non-spatial variables selected via the procedure outlined in section 2.4 and models presented in Supporting

359 Information Table S 3. Variable abbreviations are defined in Table 3

Variable	Estimate	SE	Adjusted SE	z value	<i>Pr</i> (> <i>z</i>)	CI lower	Cl upper
(intercept)	3.260	0.717	0.720	4.527	< 0.01	1.849	4.672
YG	-1.336	0.346	0.347	3.847	< 0.01	-2.017	-0.655
OG	-1.105	0.403	0.404	2.729	< 0.01	-1.898	-0.311
CF	-0.278	0.430	0.432	0.644	0.519	-1.125	0.568
рН	-0.232	0.081	0.081	2.835	< 0.01	-0.393	-0.071
gradient	-0.004	0.009	0.009	0.533	0.593	-0.022	0.012
ash density	-0.0007	0.002	0.002	0.291	0.770	-0.005	0.004
dbh13	-0.026	0.007	0.007	3.736	< 0.01	-0.040	-0.012
rgr-s	-1.174	0.729	0.730	1.606	0.108	-2.606	0.258
rgr-l	0.037	0.058	0.058	0.636	0.524	-0.077	0.152

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362 3.4 SPATIAL MODELLING

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The models resulting from the selection procedure (see Supporting Information) for the 364 prediction of ADB in 2019 by the spatial predictors outlined in Tables 1, 2 and 3 included 365 stand type and four other variables that made an independent contribution to the variation 366 between trees in their severity of ADB (Figure 5, Table 6). Greater ADB severity was strongly 367 associated with greater weighted species mingling (i.e., a lower proportion of conspecific 368 trees among the six nearest neighbours of the focal trees weighted by their species 369 richness). The sensitivity analysis showed that use of the basic species mingling index (mi6) 370 in place of the weighted index (wmi6) had a minimal effect on the model results (Tables S4 371 and S5 in Supplementary Information). It was also significantly associated with smaller 2013 372 diameter at breast height (Figure 5, Table 6). The severity of ADB was much less in the 373 young growth, old growth and especially in the managed compartment stand types than in 374 the below cliff and colluvial fan stand types. It was only very weakly associated with local 375 tree density or basal area of larger trees, and was not independently associated with size 376 dominance of the focal tree. 377

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FIGURE 5. Spatial model a) Effect (model average coefficient) of spatial predictors on adb19 severity. Single effect plots of the association of adb19 severity with each retained variable: b) stand type, c) wmi6, d) dbh13, e) lambda and f) bal. Variable abbreviations are defined in Table 3. All panels include 95% confidence intervals coloured red or green for negative or positive average effects respectively

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- **TABLE 6.** Spatial variables predicting the severity of ash dieback in 2019. Estimated regression parameters,
- standard errors (SE), z-values, p-values and confidence intervals (CI) for model averaging and composite GLMMs
- of spatial variables selected via the procedure outlined in section 2.4 and models presented in Supporting
- 391 Information Table S 4. Variable abbreviations are defined in Table 3

Variable	Estimate	SE	Adjusted SE	z value	<i>Pr</i> (> <i>z</i>)	CI lower	CI upper
(intercept)	1.157	0.386	0.387	2.988	< 0.01	0.398	1.916
YG	-1.005	0.318	0.319	3.151	< 0.01	-1.631	-0.380
OG	-0.839	0.337	0.337	2.486	0.012	-1.500	-0.178
CF	-0.041	0.431	0.432	0.096	0.923	-0.888	0.806
MCI	-2.147	0.439	0.440	4.881	< 0.01	-3.009	-1.285
MC2	-1.323	0.432	0.433	3.056	< 0.01	-2.172	-0.474
wmi6	0.777	0.357	0.358	2.169	0.030	0.075	1.480
dbh13	-0.023	0.006	0.006	3.830	< 0.01	-0.035	-0.011
lambda	-0.148	0.473	0.474	0.313	0.754	-1.078	0.781
bal	0.001	0.005	0.005	0.220	0.826	-0.009	0.011

394 **4. DISCUSSION**

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The level of ADB reached at the early-mid stage of the epidemic in Lady Park Wood was clearly linked 396 to site environment factors. The GLMM results showed that there was a very large and significant 397 difference in severity of the disease amongst the stand types occupying different topographic 398 positions and with different management histories within the woodland. The high incidence of disease 399 in the colluvial fan and below-cliff sites are as expected from previous studies reporting greater 400 infection in sites with moist soils (e.g., Muñoz et al., 2016; Havrdová et al., 2017; Skovsgaard et al., 401 2017), which is generally attributed to greater production of inoculum from litter and is associated 402 with a greater occurrence of basal lesions (Marçais et al., 2016). Topographic and substrate factors 403 may also influence crown dieback symptoms via their impact on rooting depth and drainage 404 (Skovsgaard et al., 2017). Our observations of variation amongst the topographic zones indicate that 405 trees on the lower slopes and upper steep slopes were much more severely affected than those on 406 the intermediate mid-slopes (which have greater moisture retention during drought), and there is 407 existing evidence of the importance of this moisture variation on tree ecophysiology at Lady Park 408 Wood (Peterken & Mountford, 2017). Cavin et al. (2013) studied the long-term effects of drought 409 events and found that they can lead to changes in the competition dynamics amongst the tree species' 410 populations. Given that ash is known to be susceptible to drought (Zollner & Kölling, 1994; Berger et 411 al., 2010; Dobrowolska et al., 2011; Drenkhan, Sander & Hanso, 2014) it is possible that trees on sites 412 subject to greater variation in moisture availability have reduced resistance to ADB. The low incidence 413 and significantly lower severity of ADB in the managed compartment that has been subject to recent 414 thinning is also a striking result. 415

Our first question was derived from previous research that found a clear positive association
 between higher levels of ADB and dense, unthinned stands (Skovsgaard et al., 2017; Bakys, Vasaitis &

Skovsgaard, 2013), with lower levels amongst dispersed ash trees in an agricultural matrix than within woodland at a landscape scale (Grosdidier et al., 2020). However, the results of the present study showed no marked relationship between incidence or severity of ADB and the density of trees (of all species) at the whole stand level or between severity of ADB and local tree density around individual focal ash trees calculated using a kernel function (lambda), hence our answer to the first question is 'no'.

Site and neighbourhood effects could occur through either their influence on the rate of 424 transmission of ascospores or on the resistance to infection of ash trees mediated by their 425 physiological condition. It is unlikely that, at this stage of the epidemic, spatial variation (at stand and 426 individual tree scales) in the density of *H. fraxineus* ascospores is the primary cause of the variation in 427 ADB severity of individual trees recorded in the present study within an unfragmented closed-canopy 428 woodland. This finding is strongly supported by the GLMM result showing a lack of any meaningful 429 relationship between severity of ADB and the density of ash trees in the same sub-plot as the focal 430 tree. In 2019, two years after ADB was first recorded in this well-monitored site, overall, 81% of ash 431 trees were infected, and that had increased markedly to 95% by the following summer of 2020. It is 432 likely, therefore, that the density of dispersed ascospores across the site was already so high that 433 every susceptible ash tree was subject to a high inoculum load. ADB of a single tree produces millions 434 of tiny ascospores that disperse widely even in dry conditions (estimated mean dispersal distance 0.2-435 2.6 km (Grosdidier et al., 2018)), though with a rapid decline in dispersed inoculum density up to 50 436 m from an infected host (Chandelier et al., 2014). In this context, the large differences in both infection 437 rate and, to an even greater extent, severity observed amongst the different stands in the study 438 woodland at this early-mid stage of the epidemic are notable, and the stands with the highest 439 440 percentage of trees infected and severity of ADB had only moderate or low absolute density and basal area of ash trees (Table 4). 441

442 Our second question addressed the alternative mechanism explaining variation between ash 443 trees in their severity of ADB: that their resistance to or recovery from infection is mediated by their

physiological condition, for example, earlywood vessel size and slower growth feeding back and 444 amplifying crown dieback (Klesse et al., 2020; Skovsgaard et al. 2017). To assess this, it is a unique 445 strength of the present study that Lady Park Wood has a long record of the prior growth rates of 446 individual ash trees in permanent sample plots as a valuable indicator of their condition. This revealed 447 a strong negative association between severity of ADB and relative stem radial growth rates during 448 the 11 years immediately prior to the first observation of the disease in the woodland. This provides 449 robust evidence to answer yes to the second question: trees in a more vigorous condition had greater 450 resistance to the disease. This result is compatible with earlier studies based on less precise evidence 451 that showed a negative relationship between the severity of ADB and tree "vitality" in Scandinavia 452 (Bengtsson et al., 2021; Timmerman et al., 2017), and the conclusion of Skovsgaard et al. (2017) that 453 vigorous trees can better compensate for the effects of *H. fraxineus*. Previous studies have also shown 454 that tree height can be a significant strong predictor of lower rates of ADB defoliation (Erfmeier et al., 455 2019), as well as individual tree vigour (Dobbertin, 2005), and our result that lower ADB severity is 456 significantly associated with larger diameter at breast height matches the findings of previous studies 457 (e.g., Klesse, 2021; Skovsgaard et al., 2010, Marçais et al., 2016; Enderle, Stenlid & Vasaitis 2019). It 458 may be that such a negative association between recorded severity of ADB and tree size at the earlier 459 stages of an epidemic may simply be a matter of time, with the infection taking longer to penetrate 460 all the vascular tissue of larger diameter individuals (Thomas, 2016; Erfmeier et al., 2019). Other 461 studies have suggested that in time ADB can infect ash trees of all sizes and ages (Pautasso et al., 462 2013). 463

Tree growth rates integrate many factors, including genotype, site environment and (as the basis for our third question) influence exerted by nearest neighbour trees, which may have differential impacts on resistance to ADB. The evidence for the effect of site environment factors was reviewed above. Our results provide only limited evidence that the lower the level of neighbour competition on an ash tree, the lower its severity of ADB at this stage of the epidemic. We found a quantitative indication (Figure 3) that taller ash trees with crowns scored as having canopy and sub-canopy crown

positions had much lower severity of ADB than those with crowns below the canopy, however this
was not corroborated by the spatial GLMM model result showing no association of ADB severity with
the basal area of larger trees. Therefore, our results only provide equivocal evidence for an answer of
yes to the third question.

A striking result of the spatial GLMM was that the severity of ADB was significantly positively 474 associated with a lower proportion of conspecific ash trees among the six nearest neighbour trees of 475 a focal ash tree weighted by their species richness (as shown by the weighted species mingling index, 476 and corroborated by both the strong correlation of this index with the basic species mingling index 477 and the equivalence of the model results obtained with the basic index in the sensitivity analysis). The 478 direction of this result was contrary to the expectation of the fourth question. Grossman et al. (2019), 479 in a temperate forest, and Rutten et al. (2021) in a sub-tropical forest, also reported the occurrence 480 of both positive and negative effects of a more species-diverse tree neighbourhood on the 481 susceptibility to disease of individual tree species. Keesing et al. (2006) described a suite of 482 mechanisms whereby species richness can either decrease or increase disease risk including the 483 "dilution effect" where increased density of heterospecific neighbours reduces infection rates 484 (Mitchell et al., 2002). Some other reported mechanisms can be excluded in the context of the present 485 study as *H. fraxineus* is not known to have alternative host species amongst the flora of Lady Park 486 Wood and animal vectors are not thought to be important in its transmission. Previous studies have 487 indicated a distance component of other species mixture effects. Murrell & Law (2003) postulated 488 that inter-species competition occurs at shorter distances than intra-species competition 489 ("heteromyopia") and a reversal of tree interaction effects between shorter and longer distances has 490 been demonstrated in various other contexts (Pommerening & Sanchez Meador, 2018). The evidence 491 492 available from the present study does not allow the contradiction amongst these findings to be resolved and this stands out as a priority for future research. This will be important to provide a 493 stronger mechanistic basis for the widely-held view that mixed-species stands, as opposed to 494

monocultures, have a reduced susceptibility to tree diseases (Pautasso et al., 2005), which has been
 supported by the results of a recent systematic review (Roberts et al. 2020).

There is evidence that the species identity of the near neighbours of ash trees can influence, 497 either positively or negatively, the severity of their ADB specifically (Havrdová et al. 2017). Therefore, 498 key to understanding the mechanisms of the species mingling result will be an analysis of the 499 difference in effect of individual species of neighbouring tree present at Lady Park Wood. Some 500 inference can be drawn from existing knowledge of the key species. In terms of above-ground 501 competition from the abundant canopy species it is F. sylvatica and Tilia spp. that cast the densest 502 shade (Ellenberg, 1988). The level of below-ground competition from different neighbouring species 503 is likely to interact with site substrate properties. Fagus sylvatica, an abundant species in many areas 504 of Lady Park Wood, is also highly competitive for below-ground resources, especially in certain soil 505 layers (Pretzsch et al. 2010; Bolte, Kampf & Hilbrig, 2013). It is water demanding, however as a result 506 its importance as a competitor may have been diminished due to its elevated mortality rate and the 507 long-term reduction in its growth rates following the drought of 1976 (Cavin et al., 2013). The role of 508 F. sylvatica trees as competitive neighbours is known to be complex: in old-growth forests high levels 509 of conspecific above-ground competition (shading) on F. sylvatica trees were found to reduce or even 510 reverse the negative effects of below-ground competition (Fichtner et al. 2015). 511

Instead of being a result of competition, neighbouring tree effects could be mediated by the influence of their leaf litter chemistry. For example, Havrdová et al. (2017) found that ADB severity was greater in ash trees where *F. sylvatica*, *Quercus* spp. and *Betula pendula* were present in their neighbourhood, and lower in the presence of *Abies* spp., *Pinus* spp. *and Acer* spp. They suggest that this could be explained by the interaction of different chemical and physical characteristics of the litter of different species, leading to different rates of leaf decomposition in species mixtures and a consequent effect on the degradation of ash petioles and thus ADB ascospore production.

It is therefore a priority for future research to test the relationship between severity of ADB
 and the species identity, as well as relative size, of neighbouring trees. Such evidence would indicate

the value of making greater use of NNSS based on species identity. Relative size of nearest neighbours
is, however, likely to remain the dominant factor via its effect on the vigour of the focal tree
(Pommerening & Sanchez Meador, 2018). Species identity is thus likely to be most important for
dominant "monumental" individuals in influencing the composition and spatial structure of trees in
their neighbourhood (Cholewińska et al. 2021).

The unique dataset provided by the permanent sample plots at Lady Park Wood has enabled 526 a statistical modelling procedure that provides evidence of at least four significant effects on the 527 severity of ADB of individual ash trees at this early-mid stage of the epidemic. The procedure 528 narrowed the selection of potential predictor variables and indicates the potential for the untested 529 factor of genotypic variation in resistance amongst individual ash trees (not linked to their prior 530 growth rate) to account for a high proportion of variation in their severity of infection, as well as the 531 inherently stochastic nature of the infection process. While this supports findings that there may be 532 sufficient genetic variation within the ash population on which natural selection for greater disease 533 resistance may act (Stener, 2018; Stocks et al., 2019), the notable increase in percentage of infected 534 trees between the sixth and seventh years after first detection of the pathogen in Lady Park Wood 535 (from 81% to 95%) reduces this optimism. Future monitoring will be crucial to determine what 536 proportion of the ash trees have sufficient resistance to survive the infection and subsequently set 537 seed. 538

The findings of our research have advanced those of previous studies (e.g., Grosdidier et al., 539 2020) by highlighting the influence of individual tree neighbourhood effects within mixed-species 540 forests, as well as reinforcing at an intensive population scale the findings of Klesse et al. (2021) 541 concerning a tree's previous relative growth rate as a separate effect from its size. They do not 542 543 support growing ash in tree species mixtures as an effective measure to reduce the severity of ADB. However, they do indicate the potential contribution of silvicultural measures aimed at establishing 544 species mingling patterns, and thinning targeted at reducing competition levels, based on the 545 species of neighbouring trees as well as their relative size, in addition to genetic selection, all 546

targeted at increasing the vigour of ash trees in order to increase their resistance to subsequent ADB
 infection.

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6. AUTHORS' CONTRIBUTIONS

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G.P. recorded the ash population in 2013-2015 in anticipation of ADB and was responsible with 562 many others for accumulating the earlier records. D.C. and G.P. designed the study with J.H. D.C. 563 collected most of the 2019/2020 data. D.C. processed and analysed the historic data and maps, did 564 565 all the initial data analysis and led the writing of the manuscript. J.H. advised on data analysis and contributed to writing the manuscript. A.P. advised on the selection and use of point process 566 statistics, wrote the corresponding R code and contributed to the methods section and analysis. P.L. 567 carried out the statistical procedure and GLMM modelling, and redrafted corresponding parts of the 568 manuscript. All authors contributed critically and edited the manuscript and gave final approval for 569 publication. 570

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573 7. DATA AVAILABILITY STATEMENT

All datasets are available at https://doi.org/10.5061/dryad.ngf1vhhxg.

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10.SUPPORTING INFORMATION 815

- Additional supporting information may be found online in the Supporting Information section at 817
- https://doi.org/10.5061/dryad.ngf1vhhxg. 818