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RESEARCH ARTICLE

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Estimating mortality rates of European ash (*Fraxinus excelsior*) under the ash dieback (*Hymenoscyphus fraxineus*) epidemic

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Societal Impact Statement

Damage to ash trees by ash dieback caused by the emerging fungal pathogen *Hymenoscyphus fraxineus* is impacting people across Europe. This poses challenges to: public safety; productivity of commercial forestry; green spaces and human well-being; and ecosystem services and carbon sequestration. Here, we seek to quantify the impact of ash dieback on tree mortality by analyzing surveys counting the proportion of trees that have died in sites across Europe. However, more and better data are needed to inform policy makers, foresters, conservationists, and other stakeholders as they plan for a long-term future with ash dieback.

Summary

- The ash dieback epidemic, caused by the fungus *Hymenoscyphus fraxineus*, has been present in Europe for over 20 years and caused widespread damage and mortality in ash tree (*Fraxinus excelsior*) populations. Ash is a major natural capital asset and plays an important role in nature's contribution to people in Europe.
- Here, we present a meta-analysis of surveys of ash mortality due to ash dieback, and a time-dependent model to estimate longer term mortality.
- In plantations established previous to the arrival of the epidemic, we analyze 12 surveys, finding a maximum recorded mortality of ~85%. In woodlands with exposure to ash dieback of between 4 and 20 years, we analyze 36 surveys, finding a maximum recorded mortality (which may have missed some dead trees) of ~70%. We also analyze 10 surveys of naturally regenerated saplings, finding maximum recorded mortality of ~82%. We apply logistic models to these data sets to seek longer term predictions.
- More data are needed before our models can be relied upon for policy decisions. If survival found so far in woodlands is due in part to heritable resistance, natural selection or a breeding program may allow future recovery of ash populations in Europe.

KEYWORDS

ash dieback, *Chalara*, epidemic, *Fraxinus excelsior, Hymenoscyphus fraxineus*, tree health

1 | INTRODUCTION

Over the last 20 years, an epidemic of ash dieback (ADB) caused by the fungal pathogen *Hymenoscyphus fraxineus* has swept across Europe from east to west, devastating ash tree (*Fraxinus excelsior*) populations (Pautasso, Aas, Queloz, & Holdenrieder, 2013). The epidemic is continuing to advance at invasion fronts including Norway (Solheim & Hietala, 2017), the UK (Clark & Webber, 2017), Ireland (McCracken, Douglas, Ryan, Destefanis, & Cooke, 2017), France (Marçais et al., 2017), Serbia (Keča, Kirisits, & Menkis, 2017), and Italy (Luchi, Ghelardini, Santini, Migliorini, & Capretti, 2016). A key question for foresters, conservationists, ecologists, and governments is: what percentage of existing ash trees will die in the epidemic?

Several studies in areas where ADB has been present for several years at high inoculum levels suggest that a minority of trees have low damage levels, and this apparent low susceptibility to ADB is heritable (Enderle, Nakou, Thomas, & Metzler, 2015; Enderle, Peters, Nakou, & Metzler, 2013; Lobo, Hansen, McKinney, Nielsen, & Kjær, 2014; Lobo, McKinney, Hansen, Kjær, & Nielsen, 2015; McKinney, Nielsen, Hansen, & Kjær, 2011; McKinney, Thomsen, Kjær, & Nielsen, 2012; Muñoz, Marçais, Dufour, & Dowkiw, 2016; Pliura & Baliuckas, 2007; Pliura, Lygis, Suchockas, & Bartkevicius, 2011; Pliura, Marčiulyniene, Bakys, & Suchockas, 2014; Stener, 2013). However, clear predictions of percentage mortality have proved elusive as the disease progresses slowly in mature trees (Lenz, Bartha, Straßer, & Lemme, 2016; McKinney et al., 2011), and in the early stages of infection, it is hard to distinguish resistant trees from escapees. Many new data on this topic were published in 2017.

Here, we review existing data on ash mortality in Europe, based on trees that were established prior to ADB (in both woodlands and plantations), and natural regeneration. We suggest a time-dependent model to seek to predict long-term ash mortality in the face of ADB, considering the proportion of dead trees p_D to be a function of the length of time t under ADB exposure; thus, $p_D = f(t)$. This can allow the synthesis of data across studies.

2 | DATA

Scientific journals were searched for studies reporting *F. excelsior* mortality in Europe since the first occurence of ADB. We also searched the book *Dieback of European Ash (*Fraxinus *spp.)—Consequences and Guidelines for Sustainable Management* (Vasaitis & Enderle, 2017) and references therein. We also include previously unpublished survey data from: Mendel University, Czech Republic; Kent County Council, UK; and the John Innes Centre, UK.

Studies were manually filtered to include only those where a survey year, sample size (number of assessed trees) n, and a number n_D or proportion p_D of dead ash trees were recorded. For each study that passed this filter, we also recorded, where available: study type (woodland, natural regeneration, or planted trial), country, region, tree size/age, year of first ADB detection in the region, and year of trial start. Where multiple data points had any dependency (e.g., when the same trees were surveyed over multiple time points), all data points were recorded, and this dependency noted. The full recorded data set at this stage of filtering is presented in Dataset S1.

For model fitting, data points were filtered once more. We excluded a data point that only recorded mortality during the course of one year in the middle of the epidemic. Where several data points showed dependency, only the most recent time point was carried further for model fitting, as later time points with higher mortality would be more informative for a model's predictions. Finally, in our meta-analysis, we have not included ash trials planted after the first regional detection of ADB, as it is possible that inoculation in dense nursery settings and the stress of plantation in an affected area may give levels of ADB damage that are not representative of what will occur in natural woodlands.

We initially attempted to exclude surveys of natural woodlands where there was clear evidence that some trees may have died due to ADB before the surveys began, or where dead trees may have been counted in one year but not in subsequent years due to their disappearance into the undergrowth or due to logging. However, on review of the survey methods used, we concluded that these sources of underestimation of tree mortality could have affected all studies in natural woodlands, so we decided to include all available studies, placing a general caveat over their reliability.

For each data point, we estimated years since exposure (t) based on regional year of first ADB detection, and survey year: t = Survey Year − Detection Year. The detection years we used for each region are shown in Dataset S1, together with our sources. We used the date at which an obvious wide environment outbreak was found in each region. Mortality data used for model fitting are presented in Table 1.

3 | MODEL

A two-parameter logistic model to fit the spread of infectious disease can be expressed as:

$$p_D = \frac{1}{1 + 10^{b(c-t)}} \qquad (1)$$

where b is the Hill slope of the curve and c is the point of inflection. This type of logistic model has previously been used to describe polycyclic disease progression (Madden, 1980) whereby the rate of new infections (or here $\frac{dp_D}{dt}$) is assumed to be proportional to the number of infected individuals multiplied by the number of susceptible uninfected individuals. The model assumes that all uninfected individuals are susceptible to the disease (i.e., that $p_{susceptitble} = 1 - p_D$ and therefore $\frac{dp_D}{dt} \propto p_D \cdot (1 - p_D)$), and that p_D will tend toward 1 as $t \to \infty$. This is an unrealistic assumption in the case of ADB, as several studies have found heritable low susceptibility to ADB in a minority of trees within ash populations. Moreover, previous studies have emphasised the importance of considering a maximum disease intensity <100% in logistic models of disease, not only in the prediction of

TABLE 1 Data used for model fitting (ash mortality)

Country	t	n	n_D	p_D	Reference
Woodland					
Belgium	5	268	10	0.037	Chandelier, Gerarts, San Martin, Herman, and Delahaye (2016); Chandelier, Delahaye, Claessens, and Lassios (2017)
Belgium	4.5	572	11	0.019	Sioen, Roskams, DeCuyper, and Steenackers (2017)
Estonia	11	168	29	0.173	Drenkhan et al. (2017)
Estonia	10	33	16	0.485	Lõhmus and Runnel (2014)
Estonia	10	66	26	0.394	Lõhmus and Runnel (2014)
Estonia	11	577	203	0.352	Rosenvald, Drenkhan, Riit, and Lõhmus (2015)
Germany	7	358	79	0.221	Langer, Harriehausen, and Bressem (2015); Enderle et al. (2017)
Germany	9	318	5	0.016	Langer et al. (2015); Enderle et al. (2017)
Germany	9	116	5	0.043	Langer et al. (2015); Enderle et al. (2017)
Germany	13	220	55	0.250	Langer et al. (2015); Enderle et al. (2017)
Germany	13	60	18	0.300	Langer et al. (2015); Enderle et al. (2017)
Germany	9	230	16	0.070	Lenz et al. (2016); Enderle et al. (2017)
Germany	9	585	35	0.060	Lenz et al. (2016); Enderle et al. (2017)
Italy	4	386	0	0.000	Giongo, Longa, Maso, Montecchio, and Maresi (2017)
Latvia	15	340	236	0.694	Matisone, Matisons, Laivins, and Gaitnieks (2018)
Lithuania	12	1,218	692	0.568	Pliura et al. (2017)
Lithuania	19	857	524	0.611	Pliura et al. (2017)
Netherlands	5	4,761	3	0.001	Kopinga and de Vries (2017)
Norway	6	34	1	0.029	Timmermann, Nagy, Hietala, Børja, and Solheim (2017)
Norway	6	32	0	0.00	Timmermann et al. (2017)
Norway	10	67	28	0.418	Timmermann et al. (2017)
Norway	10	52	12	0.231	Timmermann et al. (2017)
Sweden	13	330	35	0.106	Bengtsson and Stenström (2017)
Switzerland	7	201	3	0.015	Queloz, Hopf, Schoebel, Rigling, and Gross (2017)
Switzerland	6	712	14	0.020	Queloz et al. (2017)
Ukraine	5	200	0.11	0.110	Davydenko and Meshkova (2017)
United Kingdom	5	697	0	0.000	Data provided by Kent County Council
United Kingdom	5	760	6	0.008	Data provided by Kent County Council
United Kingdom	5	726	16	0.022	Data provided by Kent County Council
United Kingdom	5	362	28	0.077	Data provided by Kent County Council
United Kingdom	5	705	4	0.006	Data provided by Kent County Council
United Kingdom	5	474	61	0.129	Data provided by Kent County Council
United Kingdom	5	932	43	0.046	Data provided by Kent County Council
United Kingdom	5	171	3	0.018	Data provided by Kent County Council
United Kingdom	5	96	0	0.000	Data provided by Kent County Council
United Kingdom	5	141	28	0.199	Data provided by Edwards, Anne
Planted trials (pre-ADB)					
Czech Republic	13	1,058	844	0.798	Rozsypálek et al. (2017)
Czech Republic	13	989	740	0.748	Rozsypálek et al. (2017)
Czech Republic	13	956	815	0.853	Rozsypálek et al. (2017)
Czech Republic	13	586	450	0.768	Rozsypálek et al. (2017)
Czech Republic	13	1,243	971	0.781	Rozsypálek et al. (2017)
Denmark	12	625	341	0.546	Lobo et al. (2014)
France	6	786	22	0.028	Muñoz et al. (2016)

(Continues)

TABLE 1 (Continued)

Country	t	n	n_D	p_D	Reference
Germany	9	1915	542	0.283	Enderle et al. (2013); Enderle et al. (2017)
Germany	10	592	110	0.186	Enderle et al. (2017)
Germany	7	2,336	841	0.360	Langer et al. (2015); Enderle et al. (2017)
Germany	7	2,337	164	0.070	Langer et al. (2015); Enderle et al. (2017)
Germany	11	2,350	1,269	0.540	Langer et al. (2015); Enderle et al. (2017)
Naturally regenerated trees					
Estonia	10	2,367	0	0.00	Drenkhan et al. (2017)
Estonia	12	1591	23	0.014	Drenkhan et al. (2017)
Germany	9	698	250	0.358	Enderle et al. (2017)
Germany	7	543	206	0.379	Enderle et al. (2017)
Germany	9	489	112	0.229	Enderle et al. (2017)
Germany	9	579	79	0.136	Lenz et al. (2016); Enderle et al. (2017)
Latvia	15	7,533	755	0.100	Pušpure, Matisons, Laiviņš, Gaitnieks, and Jansons (2017)
Norway	6	64	29	0.453	Timmermann et al. (2017)
Norway	10	111	91	0.820	Timmermann et al. (2017)
Italy	4	4,486	789	0.176	Giongo et al. (2017)

Note. Data are split into woodland studies, studies performed on plantations from before the onset of ADB ("Planted trials (pre-ADB)"), and studies on naturally regenerated trees. t = time since regional ADB detection, n = number of trees surveyed, n_D = number of dead trees, p_D = proportion of dead trees.

susceptibility rates, but also for more accurate prediction of rate of disease increase (Neher & Campbell, 1992).

We therefore reasoned that it would be more appropriate to use a three-parameter logistic model, which can be expressed as:

$$p_D = \frac{a}{1+10^{b(c-t)}} \quad (2)$$

This introduces a new parameter a, which is the top asymptote of the curve. If $a < 1$, we may assume that a proportion $1 - a$ of the population has low susceptibility to ADB and will not die as a result of it. A three-parameter model has been used previously to model the incidence of ADB collar necroses over time in ash stands in south-west Germany (Enderle, Sander, & Metzler, 2017), as well as the progression of other plant diseases (e.g., Holb, Heijne, Withagen, Gáll, & Jeger, 2005; Shearer, Crane, Barrett, & Cochrane, 2007).

Data were fitted to the model using a modification (see Code S1) of the R package `nplr` (Commo & Bot, 2016). Models were fitted to minimize the weighted residual sum of squares $\sum_i n_i \cdot (\hat{p}_{Di} - p_{Di})^2$, where for each data point i, p_{Di} is the observed mortality, $\widehat{p_{Di}}$ is the fitted mortality, and n_i is the number of trees studied.

Fitted models were then assessed by calculation of a weighted goodness-of-fit (wGOF):

$$wGOF = \frac{\text{model sum of squares}}{\text{total sum of squares}} = 1 - \frac{\text{residual sum of squares}}{\text{total sum of squares}} = 1 - \frac{\sum_i n_i \cdot (\hat{p}_{Di} - p_{Di})^2}{\sum_i n_i \cdot (p_{Di} - \overline{p_D})^2}$$

where $\overline{p_D} = \frac{\sum_i n_i \cdot p_{Di}}{\sum_i n_i}$ is the weighted mean value of p_D across all observations.

In order to test the robustness of fitted models, a bootstrap approach was used. Data points used in each original model fitting were resampled with replacement. This was performed for 10,000 successful iterations (some iterations failed at the model-fitting steps due to an insufficient range of data in the resampling).

As a supplementary analysis we also fitted the data without weighting by sample size, using non-weighted residual sum of squares $\sum_i (\hat{p}_{Di} - p_{Di})^2$.

4 | RESULTS

4.1 | Ash mortality in woodland

Our pan-European dataset on mortality due to ADB in natural woodland consists of 36 data points from observations of a total of 17,825 *F. excelsior* trees. These data were from a wide range of geographical locations, including England, Ukraine, Scandinavia, the Baltic states, among others (Table 1, Figure 1a), with exposure to ADB of between 4 and 20 years. The maximum level of mortality we found recorded was 69.4% in a woodland in Latvia after 15 years of ADB exposure (Matisone et al., 2018). The site that appeared to have had the longest exposure to ADB was in Lithuania with 19 years of exposure and had 61.1% mortality (Pluira et al., 2017). These data likely do not include some trees that died and disappeared without trace.

The three-parameter logistic model (*wGOF* = 0.816 to 3 s.f., Figure 1b) gave a c (inflection point) of 10.7 suggests that mortality

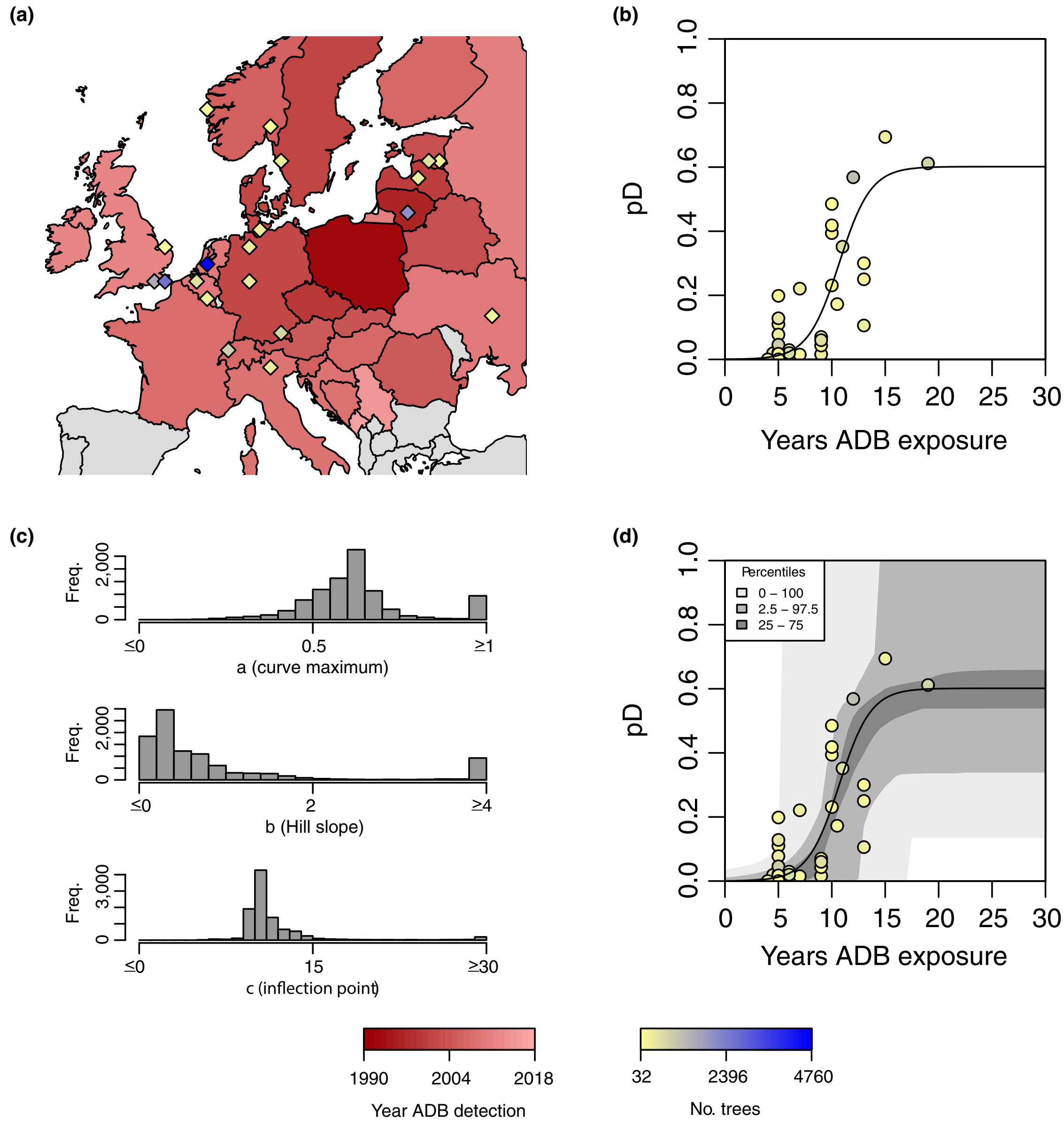

FIGURE 1 Ash mortality in woodland. (a) Approximate geographical distribution of woodlands used in studies. Where studies have pooled data from multiple sites, an intermediate coordinate was chosen. Point color corresponds to the number of trees sampled (see color scale). Ash dieback has been reported in all countries colored red, with intensity of red indicating the year in which ADB was first detected in that country. (b) A three-parameter logistic model for mortality of woodland ash trees (p_D, proportion of dead trees) over time. Data points are weighted (and points colored, see color scale) according to sample size n. Weighted goodness-of-fit =0.816. Parameters (to 3 s.f.) are *a*=0.602, *b*=0.294, *c*=10.7. (c) Parameter estimates from bootstrap. Data were resampled with replacement and a new model fitted for 10,000 successful iterations. (d) Mortality predictions based on bootstrap data. For each iteration, predictions for p_D were calculated for *t* at intervals of 0.5. Of these predictions, the range (lightest gray), the 2.5th and 97.5th percentiles (intermediate gray), and the interquartile range (darkest gray) are plotted, alongside the original model (black), as presented in panel b

rate is highest at ~10 – 11 years after exposure, and an *a* of 0.602 suggests that mortality may level off at ~60%. An analysis in which we did not weight data points by sample size gave a lower estimate for *c* and *a* (Figure S1a).

In the bootstrap analysis, 991 iterations returned errors due to lack of informative data, and were thus discarded, and resampled. Figure 1c shows the distribution of parameter values across the 10,000 bootstrap iterations. Only 908 (9.08% of total) iterations suggested that ash mortality in woodland would reach 100% (i.e., *a* was a greater than, or equal to, one (Figure 1c)).

We used the bootstrap results to make speculative predictions of ash mortality for the first 30 years following exposure (Figure 1d). A 95% confidence interval, as highlighted by the intermediate shade of gray in Figure 1d, encompasses a range of possible outcomes including 100% mortality within 15 years, and under 40% mortality after 30 years. The interquartile range of these was between 53.8% and 65.9% (3. s.f.) after 30 years.

4.2 | Ash mortality in trials planted prior to regional ADB detection

Our pan-European dataset on mortality due to ADB in planted trials established before the ADB epidemic consists of 12 data points summarizing 15,773 *F. excelsior* trees, and mostly comprises studies from Germany and the Czech Republic (Table 1, Figure 2a). The maximum level of mortality we found was 85.3% in a trial in the Czech Republic after 13 years of ADB exposure.

For planted trials, the three-parameter logistic model (*wGOF* = 0.871 to 3 s.f., Figure 2b), unlike for the woodland data, gave an *a* far greater than 1 (11.3 to 3 s.f.) suggesting that mortality will reach 100%. There is little evidence to suggest slowing of mortality over time in these trials. An analysis in which we did not weight data points gave a similar result (Figure S1b).

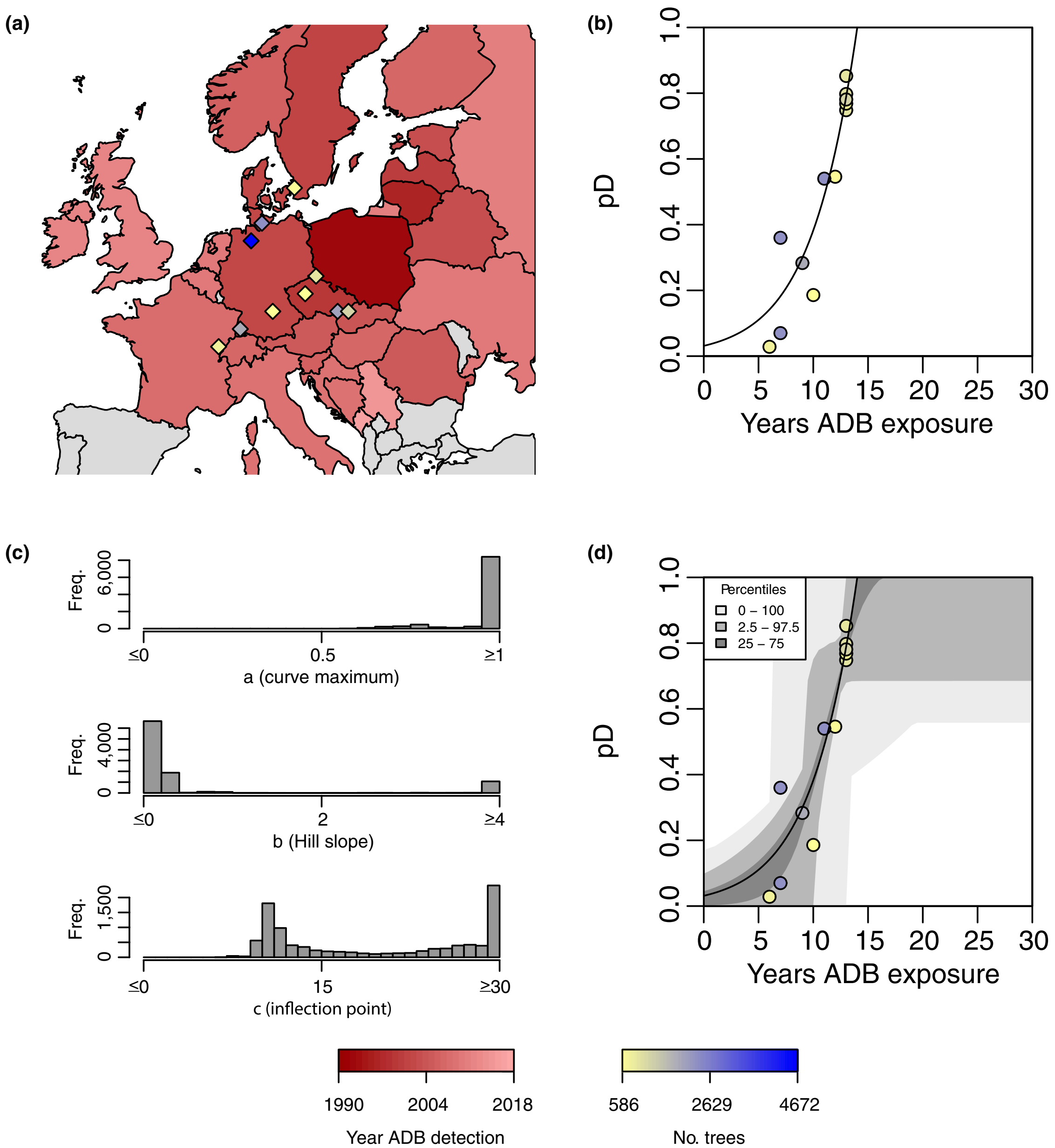

FIGURE 2 Ash mortality in trials planted prior to regional ADB detection. (a) Approximate geographical distribution of trial sites used in studies. Where studies have pooled data from multiple sites, an intermediate coordinate was chosen. Point color corresponds to the number of trees sampled (see color scale). Ash dieback has been reported in all countries colored red, with intensity of red indicating the year in which ADB was first detected in that country. (b) A three-parameter logistic model for mortality of trial ash trees (p_D, proportion of dead trees) over time. Data points are weighted (and points colored, see color scale) according to sample size n. Weighted goodness-of-fit = 0.871. Parameters (to 3 s.f.) are a = 11.3, b = 0.110, c = 23.2. (c) Parameter estimates from bootstrap. Data were resampled with replacement and a new model fitted for 10,000 successful iterations. (d) Mortality predictions based on bootstrap data. For each iteration, predictions for p_D were calculated for t at intervals of 0.5. Of these predictions, the range (lightest gray), the 2.5th and 97.5th percentiles (intermediate gray) and the interquartile range (darkest gray) are plotted, alongside the original model (black), as presented in panel b

In the bootstrap analysis (Figure 2c, d), 3,324 iterations failed. In 8,047 (80.47% of total) iterations, *a* was greater than, or equal to, 1. A 95% confidence interval, as highlighted by the intermediate shade of gray in Figure 2d, again encompasses a range of possible outcomes including 100% mortality within 15 years, and ~70% mortality after 30 years. After 30 years, all predictions within the interquartile range are 100%.

A model fitted to the combined woodland and planted trial data (*wGOF* = 0.810) showed a trend intermediate to the separate woodland and plant trial trends, levelling off at ~78% mortality (Figure 3).

4.3 | Ash mortality in naturally regenerated ash trees

Our pan-European dataset on mortality due to ADB of naturally regenerated saplings consists of 10 data points summarizing 18,461 *F. excelsior* trees, from woodlands in Italy, Germany,

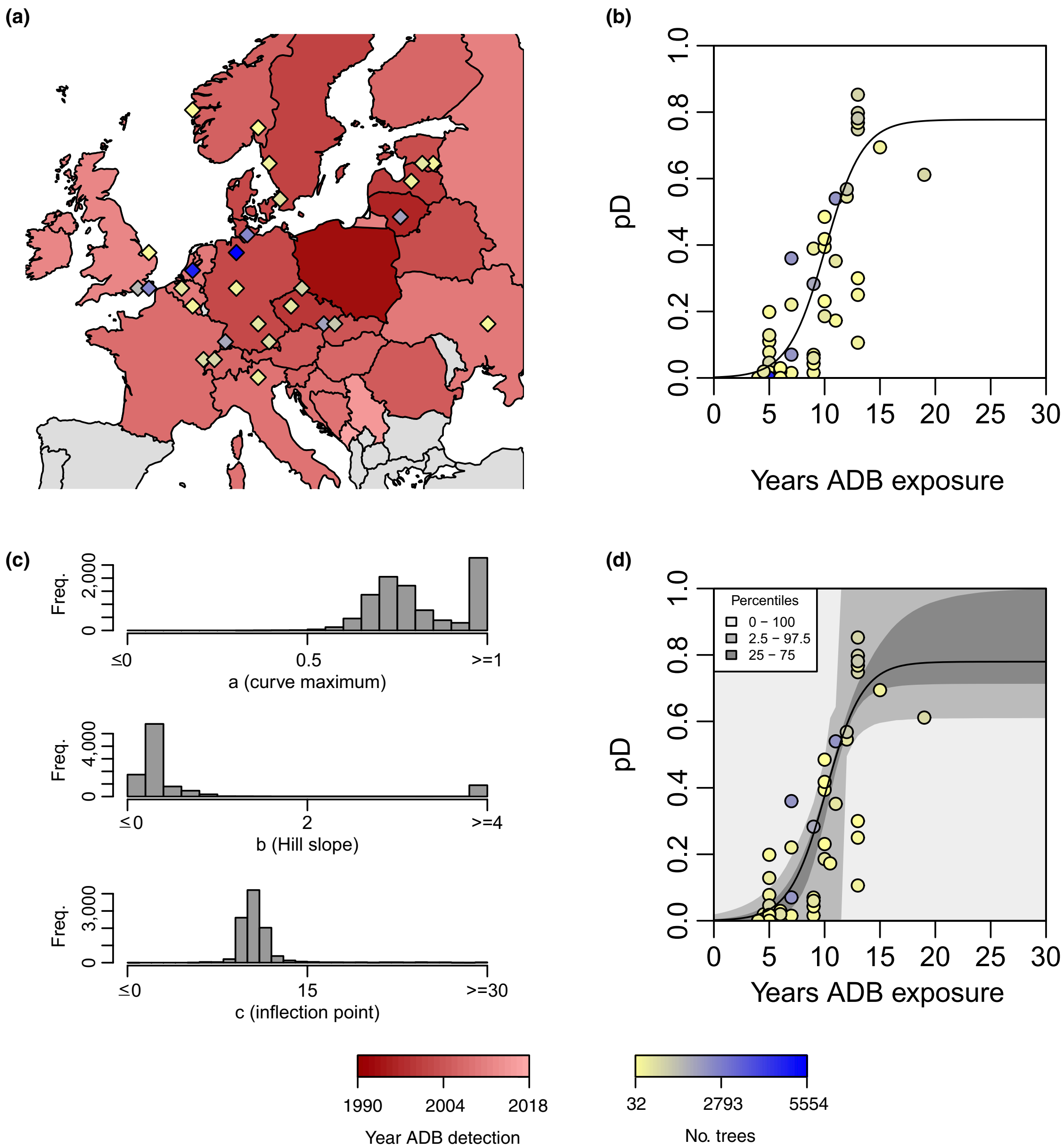

FIGURE 3 Ash mortality in both woodland and trials planted prior to regional ADB detection. (a) Approximate geographical distribution of woodlands and trial sites used in studies. Where studies have pooled data from multiple sites, an intermediate coordinate was chosen. Point color corresponds to the number of trees sampled (see color scale). Ash dieback has been reported in all countries colored red, with intensity of red indicating the year in which ADB was first detected in that country. (b) A three-parameter logistic model for mortality of woodland and trial ash trees (p_D, proportion of dead trees) over time. Data points are weighted (and points colored, see color scale) according to sample size n. Weighted goodness-of-fit =0.810. Parameters (to 3 s.f.) are a = 0.780, b = 0.263, c = 10.1. (c) Parameter estimates from bootstrap. Data were resampled with replacement and a new model fitted for 10,000 successful iterations. (d) Mortality predictions based on bootstrap data. For each iteration, predictions for p_D were calculated for t at intervals of 0.5. Of these predictions, the range (lightest gray), the 2.5th and 97.5th percentiles (intermediate gray), and the interquartile range (darkest gray) are plotted, alongside the original model (black), as presented in panel b

Norway, Estonia, and Latvia (Table 1, Figure 4a). The maximum level of mortality we found was 82.0% in a trial in Norway after 10 years of ADB exposure. Unlike the data from the mature trees analyzed above, some of the lowest levels of mortality were found in sites with the longest exposure to ADB. Indeed, there is no obvious trend in mortality over time (Figure 4b).

Model fitting to this data was not useful for inference (Figure 4): the three-parameter logistic model provided a weak fit (*wGOF* = 0.479 to 3 s.f.). In the bootstrap analysis, results (Figure 4c and 4d) show the 95% confidence interval encompassed nearly every possible outcome over a 30-year period, including 0% and 100% mortality after 30 years. Thus, we can conclude little about ash mortality over

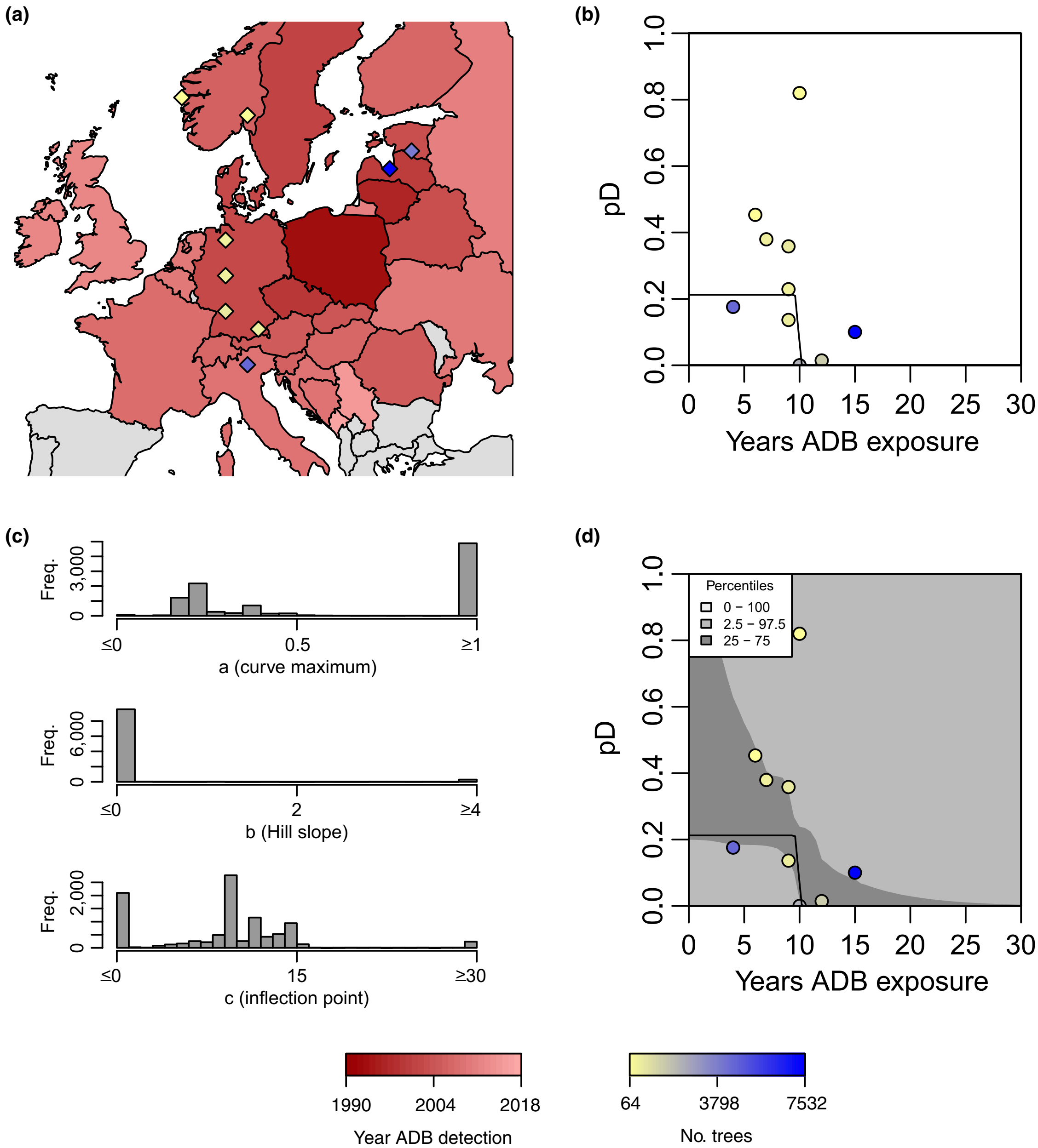

FIGURE 4 Ash mortality in naturally regenerated trees. (a) Approximate geographical distribution of woodlands used in studies. Where studies have pooled data from multiple sites, an intermediate coordinate was chosen. Point color corresponds to the number of trees sampled (see color scale). Ash dieback has been reported in all countries colored red, with intensity of red indicating the year in which ADB was first detected in that country. (b) A three-parameter logistic model for mortality of naturally regenerated trees (p_D, proportion of dead trees) over time. Data points are weighted (and points colored, see color scale) according to sample size n. Weighted goodness-of-fit = 0.479. Parameters (to 3 s.f.) are a = 0.212, b = −6.53, c = 9.90. (c) Parameter estimates from bootstrap. Data were resampled with replacement and a new model fitted for 10,000 successful iterations. (d) Mortality predictions based on bootstrap data. For each iteration, predictions for p_D were calculated for t at intervals of 0.5. Of these predictions, the range (lightest gray), the 2.5th and 97.5th percentiles (intermediate gray), and the interquartile range (darkest grey) are plotted, alongside the original model (black), as presented in panel b

time in naturally regenerated trees, except that the data available seem to suggest a different trend to the rise in mortality displayed in mature woodland trees (Figure 1).

5 | DISCUSSION

The number of reliable datasets recording ash mortality across Europe due to ADB is surprisingly small given the level of public and scientific interest in this epidemic. The available datasets were collected by different researchers, and we do not know how every study site was selected, and we do not have systematic information about their biotic and abiotic environmental variables. Some researchers may have deliberately chosen woodland sites that had high mortality, whereas others may have chosen woodlands with unusually low mortality. Our estimates of time of exposure to ADB may be inaccurate, as we relied on first reports of a wide environment outbreak in different regions. Wylder, Biddle, King, Baden, and Webber (2018) have shown through tree-ring dating of lesions that ADB was present in the UK in isolated ash plantations several years before an obvious wider environment outbreak was detected, but we do not have equivalent data for all regions in our study. We expect that all surveys of woodlands may have missed some dead trees that disappeared without trace either before surveys started, or between years of surveys. Finally, the lack of data for trees with longer exposure times makes it difficult to accurately predict the precise trajectory of mortality in ash populations. Together, this means that our analyses are based on a low number of data points and our predictions from these data points have considerable uncertainty. Nonetheless, we can draw some useful conclusions from this dataset. Three useful observations can be made from the raw data alone, without relying on our models.

First, it is notable that no site has yet reached 100% mortality, even after 20 years of exposure to ADB. The worst affected site—a plantation—had 85% mortality. This means that even with the most pessimistic view of the ADB epidemic, we cannot be certain that 100% of ash trees in Europe will die. However, in those studies that examined the health of the surviving trees, only a small minority are fully healthy. Even if trees do not die from ADB, their growth and reproduction are diminished, and this reduces their value in terms of both ecological function and forestry yield.

Second, natural woodlands are currently showing lower levels of mortality in Europe than planted trials that were established before the ADB epidemic was found. We do not know the reason for this, but possible explanations could be as follows: (a) Some dead trees are likely to have disappeared without trace in woodlands, but this is less likely to happen in planted trials where trees are regularly spaced and often tagged. (b) It could be that ash trees in natural woodlands have better local adaptation to their sites, and so are more resilient in the face of disease threats. (c) It could be that woodland sites contain a greater diversity of other microorganisms associated with ash than plantations, which compete with or are detrimental to *H. fraxineus*. (d) It could be that a diversity of other tree species in woodlands help to reduce the spread of inoculum or the growth of *H. fraxineus*. (e) It could be that the leaf canopy is higher in natural woodlands, reducing the levels of inoculation from *H. fraxineus* fruiting bodies on the ground. (f) It could be that the average age and size of ash trees is greater in natural woodlands and they therefore take longer to die from ADB. Some or all of these factors could be playing a role in the lower mortality of woodland trees. We do not know if the latter five factors would merely slow the rate at which ash trees die in woodlands, or cause the number of dead trees to plateau over time.

Third, it appears that natural regeneration lacks the mortality trajectory of mature trees under ADB pressure. Remarkably, three data points from the Baltic states show very low mortality in natural regeneration after 10 years or more of the ADB epidemic, one of them with zero recorded mortality. Sampling structure of the natural regeneration data is inherently different to that of mature trees, in that new natural regeneration occurs every year. We could speculate that increased numbers of surviving natural regeneration could occur for at least two reasons: (a) Inoculum pressure may be falling in woodlands as ash trees die, meaning that more seedlings escape infection. (b) Natural selection may be acting at an early stage on ash seedlings, allowing only those that have low susceptibility to ADB to survive to be saplings; this has been suggested by Enderle et al. on the basis of their data, which we have included in this meta-analysis (Enderle et al., 2017). However, our natural regeneration dataset is too small for firm conclusions to be drawn.

While the three observations above can be derived from our raw data alone, the models that we have fitted to these data may allow us to make predictions about the future of ash populations in Europe. The model for data from natural woodlands cannot exclude the possibility of 100% mortality within 30 years, but predicts that mortality between 50% and 75% is more likely given the current available data. In planted trials, the model predicts 100% mortality in future given the current available data. Regarding natural regeneration, the fit of the model is so poor that we cannot make predictions. There is a clear need for more, longer term, and better data on ash mortality under ADB in both woodlands and planted trials before reliable predictions can be made about the future.

The percentage of living trees that are still to be found in the sites included in this meta-analysis, including in areas with long exposure to ADB is somewhat encouraging if we take a long-term perspective. If this survival is due to heritable resistance, a breeding program, or the long-term effects of natural selection, may allow more resistant ash trees to spread in Europe. Even if these more resistant trees eventually die due to ADB, their longevity under ADB inoculum pressure may be due to heritable partial resistance, which means their offspring may have increased resistance, especially if they have successfully crossed with other less susceptible trees in their local area. Although we may witness terrible devastation of ash woodlands in Europe, our grandchildren may see viable ash populations.

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AUTHOR CONTRIBUTIONS

T. C. and R. J. A. B. planned and designed the research and wrote the manuscript. T. C. analyzed the data and constructed the models. J. R., A. E., L. B. and T. H. contributed data.

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