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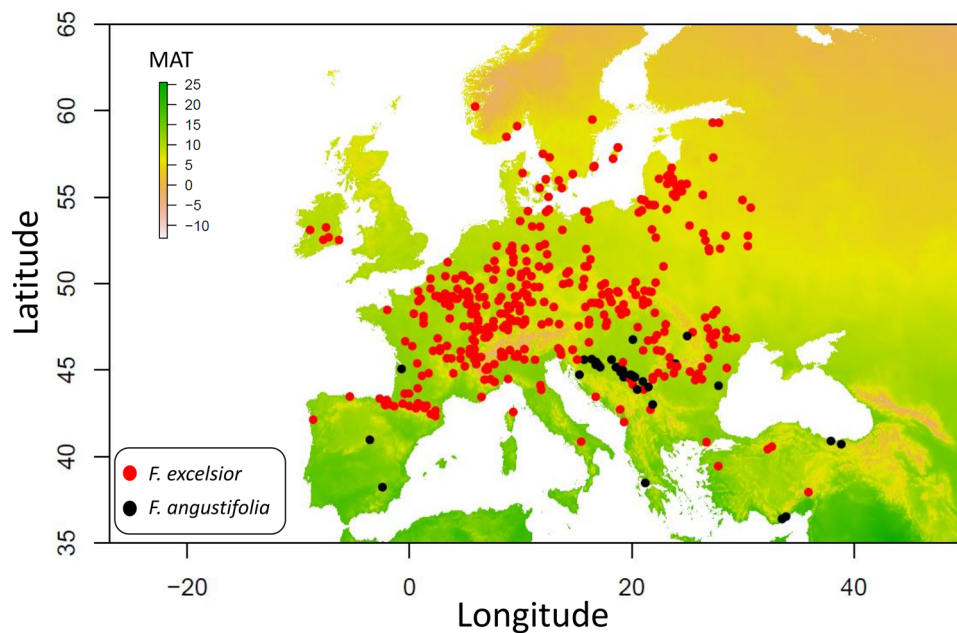
## European-wide forest monitoring substantiate the necessity for a joint conservation strategy to rescue European ash species (*Fraxinus* spp.)

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European ash (*Fraxinus excelsior*) and narrow-leaved ash (*F. angustifolia*) are keystone forest tree species with a broad ecological amplitude and significant economic importance. Besides global warming both species are currently under significant threat by an invasive fungal pathogen that has been spreading progressively throughout the continent for almost three decades. Ash dieback caused by the ascomycete *Hymenoscyphus fraxineus* is capable of damaging ash trees of all age classes and often ultimately leads to the death of a tree after years of progressively developing crown defoliation. While studies at national and regional level already suggested rapid decline of ash populations as a result of ash dieback, a comprehensive survey at European level with harmonized crown assessment data across countries could shed more light into the population decline from a pan-European perspective and could also pave the way for a new conservation strategy beyond national borders. Here we present data from the ICP Forests Level I crown condition monitoring from 27 countries resulting in > 36,000 observations. We found a substantial increase in defoliation and mortality over time indicating that crown defoliation has almost doubled during the last three decades. Hotspots of mortality are currently situated in southern Scandinavia and north-eastern Europe. Overall survival probability after nearly 30 years of infection has already reached a critical value of 0.51, but with large differences among regions (0.20–0.86). Both a Cox proportional hazard model as well as an Aalen additive regression model strongly suggest that survival of ash is significantly lower in locations with excessive water regime and which experienced more extreme precipitation events during the last two decades. Our results underpin the necessity for fast governmental action and joint rescue efforts beyond national borders since overall mean defoliation will likely reach 50% as early as 2030 as suggested by time series forecasting.

European ash (*Fraxinus excelsior*) and narrow-leaved ash (*F. angustifolia*) are key forest tree species with high ecological and economical value for the European forest sector<sup>1</sup>. As light demanding pioneer species, they successfully inhabit a wide range of different ecosystems including riparian forests and mountain forests amongst others<sup>2</sup>. Their ability to particularly tolerate temporary flooding makes them both indispensable components of alluvial forests with strongly fluctuating hydrological regimes<sup>3</sup>. Moreover, both ash species are host to a wide range of other taxa including mammals, birds, invertebrates, and bryophytes. As such, Mitchell et al.<sup>4</sup> estimated that from 953 species associated with European ash, 69 can be characterized as being “highly associated” with its host, which means that these species will be under threat of becoming rapidly extinct when the host populations decline.

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**Figure 1.** Overview of analysed survey plots from the ICP Forests Level I dataset.

However, European ash and narrow-leaved ash are currently endangered, since the invasive pathogen *Hymenoscyphus fraxineus* (T.Kowalski) Baral, Queloz & Hosoya has entered Europe around 1990<sup>5</sup>. The disease is commonly known as ash dieback (hereafter abbreviated with “ADB”) and has devastatingly spread over entire Europe throughout the last 30 years<sup>6</sup> with an expansion velocity of 30–70 km per year<sup>7–10</sup>. The epicentre of the disease is thought to be located in north-eastern Poland and has concentrically expanded through wind-dispersed ascospores as well as by human activity<sup>11</sup>. Briefly, leaves of ash trees are infected by windborne ascospores from where the fungus spreads via the petiole-shoot junction into the woody tissue of the tree. Recurrent infections cause rapid crown decline which often leads to mortality of trees after a few years<sup>12</sup>. Both species are thought to be equally susceptible against ADB<sup>12</sup>, while *Fraxinus ornus* as the third ash species occurring in Europe seems to be more resilient against the disease<sup>13</sup> and is hence not considered in this study.

The extent to which the European population of *F. excelsior* and *F. angustifolia* has been declining since the arrival of the pathogen is largely unknown, which makes targeted conservation efforts at pan-European level challenging. National and regional reports on mortality rates were so far based upon literature reviews<sup>14</sup>, experimental forest sites<sup>15,16</sup>, and national forest inventory data<sup>17–19</sup>. However, the different approaches, datasets, and their specific sampling biases make it difficult to draw a conclusive pattern for European ash and narrow-leaved ash across their entire distributions. In particular, mapping mortality rates in space and time for entire Europe across the last three decades based on a consistent dataset could inform conservationists and policy makers at national and international levels about the current status of ash and can unravel mortality hotspots which should be given the highest priority for rescue and conservation programs in the near future. In this study we make use of survey data from the ICP Forests Level I network, providing detailed information on crown condition and diseases in annual resolution since 1987<sup>20</sup>. In total, we analyzed 36,170 observations on ash trees from 1987 to 2020 in 27 countries and incorporated stand information as well as climate data in order to test for covariation between ash dieback-induced mortality and ecological variables that may accelerate or decelerate the decline as was recently suggested in earlier studies at regional scale<sup>17,19,21</sup>. We hypothesize that the mortality of both ash species has significantly increased throughout the last three decades resulting in a devastating ash dieback driven by ADB rather than by other abiotic and biotic agents. Moreover, we hypothesize that moist growing conditions, high abundance of ash, and moist weather conditions exacerbate mortality as they are likely to provide optimal growing conditions for the pathogen. Finally, we aim to use the past defoliation history to forecast the near future and unravel critical points for the long-term vitality and persistence for both species.

## Results

**Observed mortality and defoliation across Europe between 1987 and 2020.** We identified 407 plots across 27 countries in which European ash or narrow-leaved ash occurred since the start of the survey in 1987 (Fig. 1, Table 1). This resulted in a total of 36,170 observations (plots × trees × years). Between 1987 and 2000 mortality frequency was moderate and occurred only sporadically in Spain, France, Romania, Slovakia, Italy, Lithuania and Moldova (range 0.006–0.15). Nevertheless, one stand in Belarus already showed 100% mortality between 1987 and 2000 (Fig. 2). Between 2000 and 2010 mortality accelerated mainly in Poland, Lithuania, Belarus, Sweden, Denmark, Germany, Czech Republic and at some local spots in France. While in most of these countries mortality rates were still low (1 to 3%), Poland and Sweden already showed significant mortality within stands (10% to 100%). However, in the following decade (2010–2020) ash mortality significantly accelerated

Country	Region	Plots	Trees	Observations (trees × years)	First observation of ADB <sup>a</sup>	Comment
Austria	East	5	16	223	2005	Last year of Level I monitoring: 2010
Belarus	East	12	60	694	1996	No data submission after 2015
Belgium	West	4	15	182	2010	
Croatia	South	13	123	1911	2009	
Czech Republic	East	18	123	1108	2004	
Denmark	North	4	35	658	2003	
Estonia	East	2	5	106	2003	
France	West	91	663	10,534	2007	
Germany	East	62	443	6087	2002	
Greece	South	1	19	38	not yet arrived	
Hungary	East	5	16	205	2007	
Ireland	West	5	35	69	2012	No data submission 2013–2018. Data on ash only in 2019–2020
Italy	South	22	109	1297	2009	
Latvia	East	2	6	48	2000	
Lithuania	East	14	85	985	1996	
Luxembourg	West	2	5	88	2010	
Moldova	East	6	103	543	No estimate	No data submission 2002–2016, and 2019–2020
Montenegro	South	2	6	54	2015	
Norway	North	3	4	4	2006	No data on ash before 2013. 5-year rotation from 2013 onwards. No defoliation assessments on ash
Poland	East	19	90	690	1992	
Romania	East	34	142	2347	2005	
Russia	East	5	20	48	2003	No data submission after 2011
Serbia	South	16	137	1604	2015	
Slovakia	East	12	130	3258	2004	
Slovenia	South	5	7	42	2006	
Spain	South	12	117	1916	2021	<sup>27</sup>
Sweden	North	11	67	567	2001	No data submission 2007–2008. 5-year rotation from 2009 onwards. No defoliation assessments on ash after 2006
Switzerland	West	11	41	679	2008	
Turkey	South	9	21	185	Not yet arrived	First year of Level I monitoring: 2007
Total		407	2643	36,170		

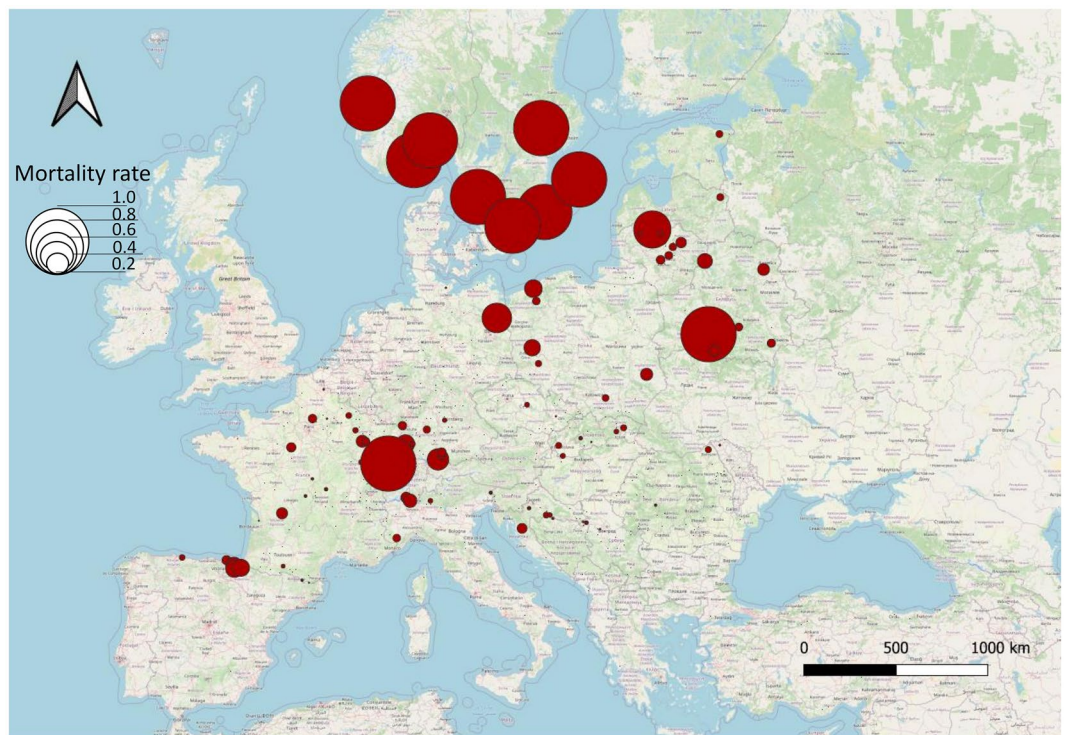
**Table 1.** Summary of observations by country. <sup>a</sup>The dates of first arrival of ADB were compiled from national reports in Vasaitis and Enderle<sup>6</sup>.

with observed mortality in nearly all parts of Europe. Most notably, southern Scandinavia became a mortality hotspot with eight stands where all ash trees died within this period.

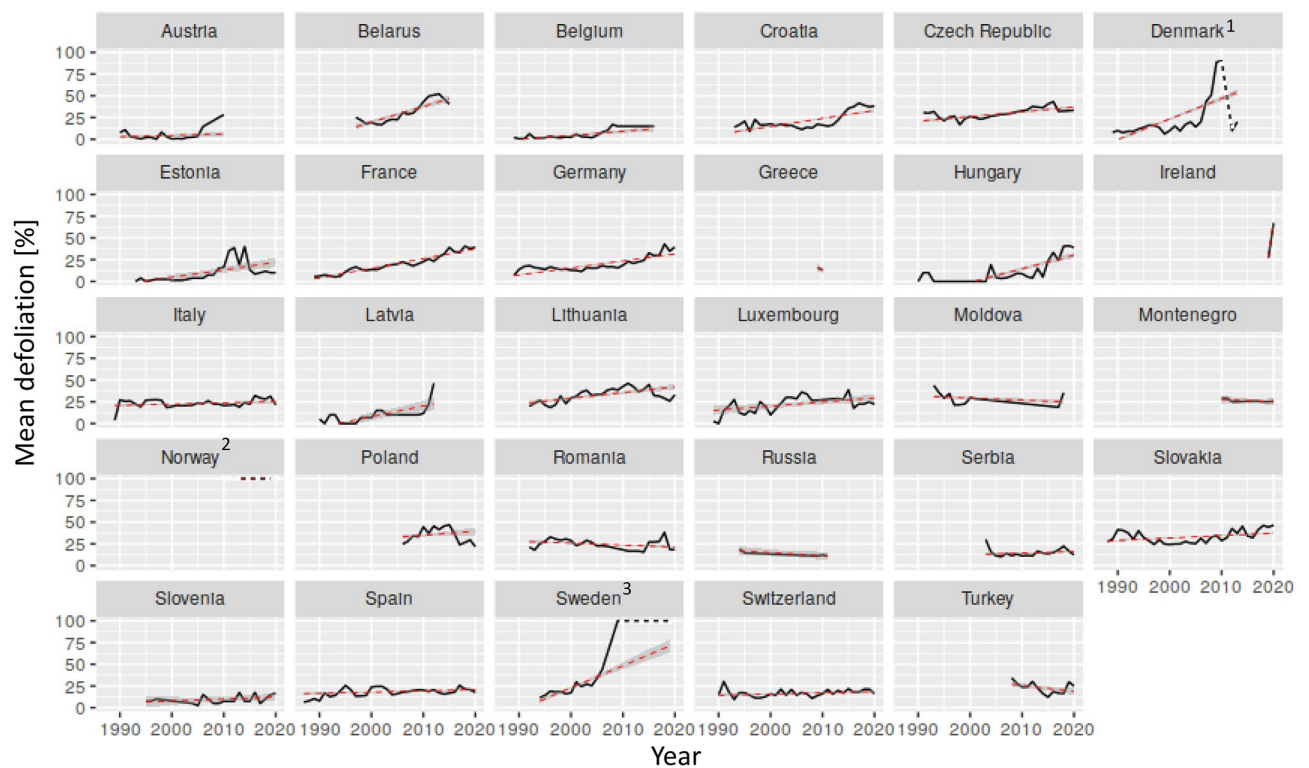
Generally, crown conditions of ash trees became progressively worse since the beginning of the survey across the entire range of occurrence. While average defoliation was 15% until the year 2000, it already reached 25% in 2010. After the latest survey in 2020 mean defoliation of European ash and narrow-leaved ash has reached 38% on average. Mean defoliation showed strongest increase in the eastern, northern, and central part of the distribution since 1987 (Belarus, Denmark, Estonia, Latvia, Lithuania, Poland, Sweden, Germany, France, Luxembourg, Slovakia), and mostly non-significant trends in the southern part (Croatia, Moldova, Romania, Serbia, Slovenia, Spain, Switzerland, Turkey) (Fig. 3).

**Survival probability after 30 years of infection history.** The two different survival models (simultaneous/non-simultaneous infection) gave similar results for the first 10 years after infection, but diverged right after that period. After 20 years of infection model 1 which assumed an equal start of infection for all ash populations estimated a much higher survival probability of 0.95 (95% CI 0.939–0.959) while model 2 (assuming that infection happened delayed) estimated an overall survival probability of 0.7 (0.607–0.734). Overall survival probability after the last assessment of trees in 2020 was 0.84 (0.823–0.858) for model 1 and 0.5 for model 2 (0.404–0.628). The Kaplan-Maier step functions for both models are shown in Fig. 4.

**Cox proportional hazard model & Aalen additive regression model.** Both the Cox-model and Aalen additive regression model unraveled significant covariates which determined survival of ash trees. The Cox-model found a significant influence of water status ( $p < 0.01$ ) and a highly significant influence of extreme precipitation events ( $p < 0.001$ ) as determinants for survival. Hazard ratios indicated that mortality risk increases towards sites having higher amount of excess water and also towards locations that have experienced more months with extreme precipitation during the last decades (Table 2). In concordance, the Aalen additive regres-

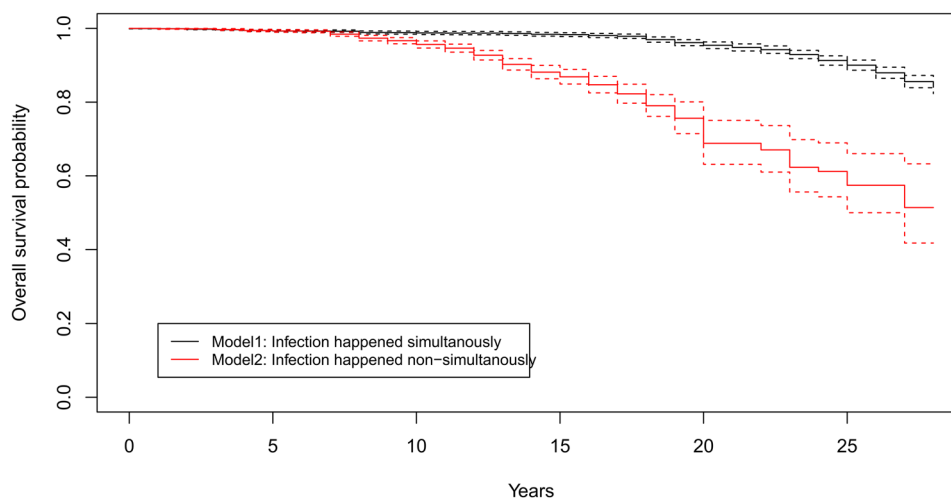


**Figure 2.** Cummulative mortality rate of ash between 1987 and 2020.



**Figure 3.** Mean defoliation across plots by survey country. Red dashed line shows linear time-series trend.  
<sup>1</sup>Note that the downward trend in Denmark is caused by loss of of some plots and does not show recovery.  
<sup>2</sup>Norway assessed ash only since 2013 and only dead trees were recorded without defoliation. <sup>3</sup>Sweden changed its survey rotation since 2009 and only dead trees were recorded since then in 5 year intervals.





**Figure 4.** Kaplan-Maier survival function and overall survival probabilities for two different models (black: infection started in 1992 regardless of country, red: infection happened delayed with distinct infection timepoints in European countries). For Model 2 we assumed infection start of single countries according to dates of first arrival published in Vasaitis & Enderle 2017.

Model covariate	Baseline hazard	Hazard ratio	se	z	Pr(> z )	Lower 95	Upper 95
<b>Water status</b>	<b>0.588</b>	<b>1.800</b>	0.223	<b>2.643</b>	<b>0.00823**</b>	<b>1.164</b>	<b>2.784</b>
Humus type	0.174	1.190	0.114	1.534	0.12504	0.9528	1.487
Ash density	0.054	1.055	0.367	0.146	0.88355	0.5136	2.168
Max. temp.>0	0.056	1.058	0.384	0.147	0.88348	0.4987	2.244
Max. temp.<0	- 0.295	0.744	0.164	- 1.798	0.07224	0.5395	1.027
<b>Extreme rainfall surplus</b>	<b>0.151</b>	<b>1.163</b>	<b>0.043</b>	<b>3.54</b>	<b>0.0004***</b>	<b>1.0699</b>	<b>1.265</b>
Extreme rainfall deficit	- 14.900	0.000	2743.000	- 0.005	0.99567	0	Inf

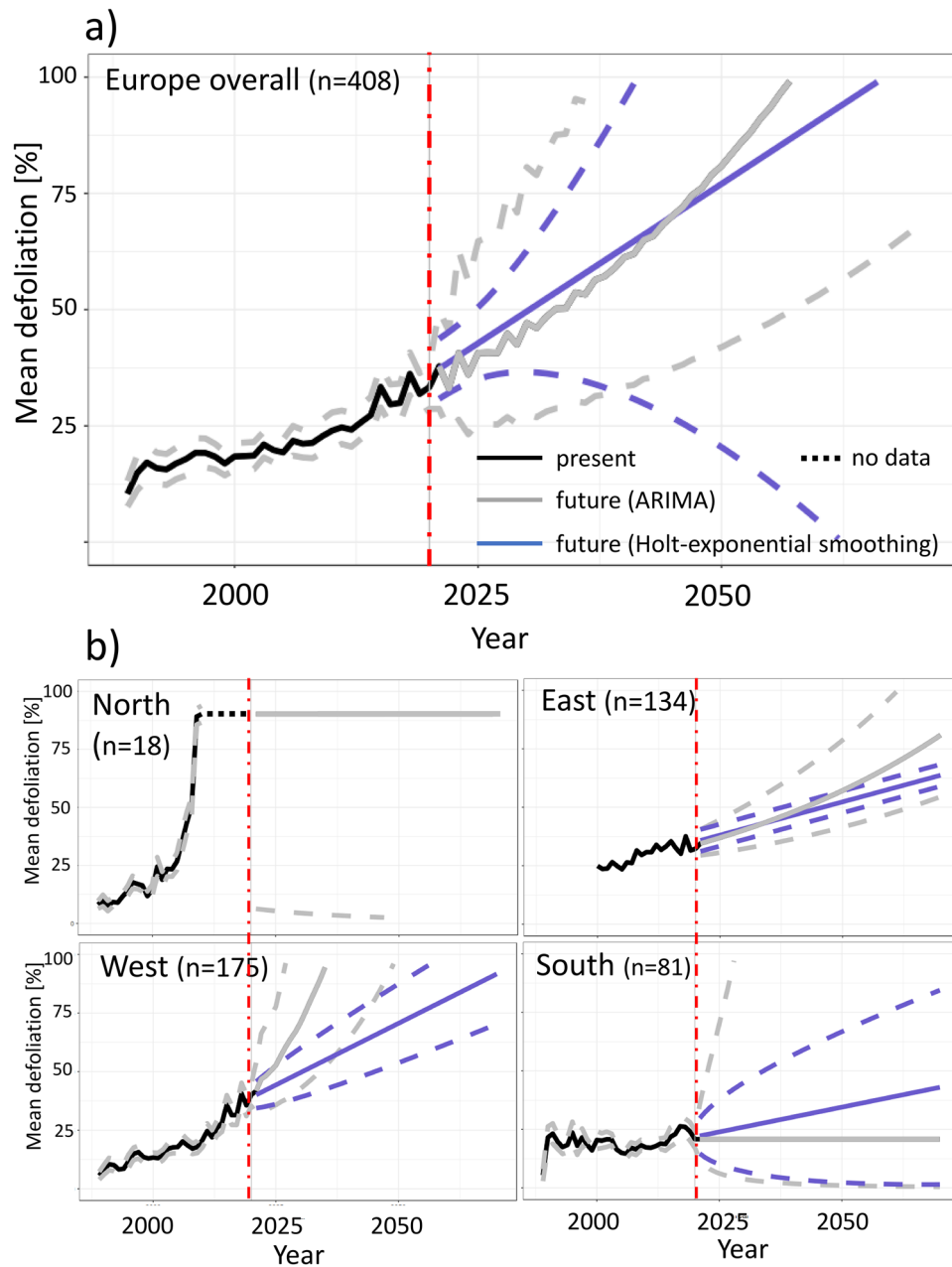
**Table 2.** Summary statistics from the Cox hazard model. Significant covariates are marked in bold. \*\* significant at  $p < 0.01$ , \*\*\* significant at  $p < 0.001$ .

Model covariate	Slope	Hazard	se	z	p
Intercept	- 0.024	- 0.002	0.001	- 1.895	0.058
Water status	0.006	0.001	0.000	1.231	0.218
Humus type	0.002	0.000	0.000	1.358	0.175
Ash density	- 0.001	0.000	0.001	0.066	0.948
<b>Max. temp.&gt;0</b>	<b>- 0.007</b>	<b>- 0.001</b>	<b>0.000</b>	<b>- 2.372</b>	<b>0.018*</b>
Max. temp.<0	- 0.001	0.000	0.000	0.164	0.870
<b>Extreme rainfall surplus</b>	<b>0.002</b>	<b>0.000</b>	<b>0.000</b>	<b>2.900</b>	<b>0.004*</b>
<b>Extreme rainfall deficit</b>	<b>- 0.014</b>	<b>- 0.002</b>	<b>0.000</b>	<b>- 4.278</b>	<b>0.000***</b>

**Table 3.** Summary statistics from Aalens additive regression model. Significant covariates are marked in bold. \* significant at  $p < 0.05$ , \*\*\* significant at  $p < 0.001$ .

sion model revealed a strong negative impact of extreme precipitation events (slope: 0.003;  $p < 0.01$ ), but also a compensating effect of extreme drought events (slope: -0.012;  $p < 0.01$ ). Effect sizes of these two covariates were moderate and appeared mainly at time periods between 15 and 20 years after infection (Table 3; Supporting information S1).

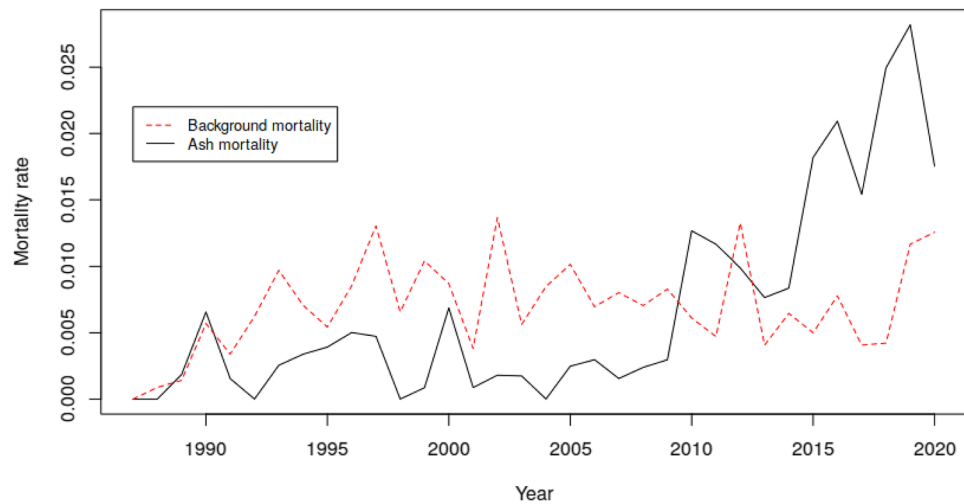
**Time-series forecasting of crown condition development.** Both estimators (ARIMA, exponential smoothing) gave similar forecasting results with continuously increasing defoliation until the end of the forecasting period (2071) and strongly suggested that approximately until the year 2030 (exponential smoothing: 2031, ARIMA: 2033) mean defoliation could reach a critical threshold of 50% (Fig. 5). Confidence intervals were gen-



**Figure 5.** Time-series forecasting of mean defoliation per plot for (a) entire Europe and (b) at regional scale. Dashed lines show 95% confidence intervals. Holt exponential smoothing did not give meaningful results for Scandinavia and is therefore not displayed in the northern subplot.

erally narrower for the ARIMA model compared to exponential smoothing until 2036, but continuously increased after that time point towards more uncertain estimates. Both models were evaluated against the last ten years of observations (2010–2020) and exhibited high correlation between observed and forecasted data (Pearson-moment correlation 0.82 and 0.84, respectively). The ARIMA model showed generally better goodness-of-fit between observed and forecasted data with a MSE of 6.6% versus 16% (Supporting Information S2).

**Mortality of ash versus background mortality.** Mortality of ash trees was largely decoupled from background mortality within the same plots (Fig. 6). As already outlined above some mortality occurred in southern Europe in 1990 probably as a result of abiotic factors and therefore strongly correlated with background mortality. Throughout the remaining period there was literally no correlation between mortality of ash and background mortality ( $r=0.15$ ). Since 2010, ash mortality clearly accelerated and exceeded background mortality. By the end of 2020 10.8% of all surveyed ash trees had died while background mortality in the same plots was only 0.7%.



**Figure 6.** Correlation between ash mortality and background mortality by survey year. Note that data was aggregated over all plots regardless of country or region for purposes of illustration.

## Discussion

Mortality of ash has clearly accelerated during the last three decades and has already reached a catastrophic peak in northern Europe where a large majority of ash trees have disappeared from active survey plots by the end of 2020. This is also in agreement with an estimated overall survival probability of 0.2 after nearly twenty years of infection history in this region. The numbers reported here could even represent the most optimistic estimate for survival of ash in Scandinavia, since some of the plots in Sweden and Denmark showed already severe crown defoliation before annual assessments were cancelled (Supporting Information S3). As an example, plot #55 from Denmark harboured 23 ash trees which had almost 95% defoliated crowns before the plot was abandoned in 2010 and most of the trees had meanwhile died. (Dr. Iben Margrete Thomsen, University of Copenhagen, pers. communication). Our observations are in concordance with local and regional surveys from national forest inventories, which reported massive decline of European ash in Southern Scandinavia in recent years. Solheim and Hietala<sup>22</sup> monitored the progress of ash dieback in south-western Norway since 2008 and estimated a spread velocity of 51 km per year. Diaz-Yanez et al.<sup>17</sup> investigated survival of European ash in Norwegian forest inventory plots and found a 74% increase in mortality rate after the disease has become prevalent in Norway. Although the Norwegian plots in our study are generally characterized by very low frequency of ash, the results can nevertheless be interpreted as a strong argument for the efficient and devastating spread of ash dieback, because the fungus seems not to depend on high host density in order to conquer new territory quickly. Also in Denmark and Sweden European ash began to disappear rapidly after the disease arrived in 2003 and 2001, respectively<sup>15,23,24</sup>. In Sweden *F. excelsior* became red-listed in 2010 and later even reached the status “critically-endangered”<sup>15</sup>. Consequently and in concert with the results presented here, the evidence strongly suggests that *Fraxinus excelsior* is currently under extreme extinction risk in northern Europe.

Furthermore, other hotspots of ash mortality are currently situated in the Baltic region (Lithuania, Poland), in eastern Europe (Belarus), north-eastern and south western Germany, as well as in eastern France (Fig. 2). Although not as severe as in the northern part, our results clearly demonstrate that the disease is establishing across all of Europe, which was also very recently confirmed by national forest inventory data<sup>19</sup>. Since the Baltic and eastern countries were the first which came in contact with the disease in the beginning of the 1990s, the pattern may be unanticipated and one would expect highest mortality in these countries rather than in the north or in the west. One explanation for this could be that the density of survey plots in which ash occurs are lower in the eastern part compared to the west (134 vs. 175). This is indeed true for Estonia and Latvia, for instance, where European ash is most likely underrepresented when compared to data from national forest inventories. The second explanation could be that assessment schemes in some eastern countries were harmonized a little later and therefore some trees were probably already gone when the survey started. As an example, Poland started to assess European ash first in 2006 when the disease had already been affecting stands for more than 15 years which could be the reason for the observed discrepancy.

Southern Europe seems to suffer least from ash dieback since mortality rates are still low and happened only sporadically. Mortality in northern Spain and southern France which occurred early at the beginning of the survey was certainly not related to ash dieback, since both areas were free of the disease at that time<sup>25</sup>. Besides the fact that the infection history of Southern Europe is still short and therefore may have caused higher survival, abiotic reasons such as higher temperatures, lower rainfall and generally drier site conditions could have contributed as well as they may inhibit fungal growth<sup>21,26</sup>. Nevertheless, *H. Fraxineus* was very recently also identified for the first time on ash trees in north-western Spain<sup>27</sup> and therefore we have to assume that the disease is still in its most infantile stage in the Southern region.

In general, mortality of ash during the last three decades was largely decoupled from background mortality and therefore unlikely to be caused by other biotic or abiotic reasons such as drought, storms, and others (Fig. 6). As already mentioned, only the very first incidences of mortality in 1990 were co-occurring with mortality in other species and therefore are not attributable to ash dieback. Since 2010 the European-wide mortality of ash has even exceeded background mortality and is continuously rising, while background mortality in the same plots remains constant. This demonstrates that in fact the majority of all cases in which ash trees are currently dying can be assigned to ash dieback as the predominant cause of death. Although the specific cause of crown damage in the ICP Forests Level I data can generally be retrieved down to the species level in the case of fungal agents (e.g. *Hymenoscyphus fraxineus* as the main causal agent of ash dieback), it is difficult to incorporate such data in detailed analyses, since the specific cause was hardly assessed and often not recognized in the very early years of the infection history and given that the damage coding system was first introduced in 2005. Nevertheless, *H. fraxineus* (or *Chalara fraxinea* as its asexual stadium is named) is currently accounting for 53% of all damage causes where a specific biotic agent can be determined (data not shown). This corresponds to approximately every fourth ash tree in the survey (23.4%) which is already carrying the disease by 2020.

We aimed to assess the overall survival probability of ash after an exposure time of 28 years to ash dieback in order to provide meaningful planning horizons for conservation and ecosystem management. We found that the probability of survival was much lower when the exposure time—approximated by the first observation of ADB at national levels—was corrected for the infection history, since the disease spread concentrically from north-eastern Poland to other regions in Europe. The assumption that entire Europe was simultaneously infected in 1992 is too simplistic and would have caused much longer time spans from infection to death for regions further apart from the epicentre. This, in turn, generated much higher survival probabilities compared to the more realistic scenario of shifted infection history.

We estimated that the overall survival probability of ash after nearly three decades of exposure is approximately 50%, but with large differences among regions (e.g. northern group: 0.2, southern group: 0.8). Coker et al.<sup>14</sup> estimated that mortality of ash in woodlands after 11 years of exposure reaches a maximum at 60% and remains constant afterwards. Although the values from Coker et al.<sup>14</sup> and those from our study cannot directly be compared due to methodological differences, such a trend cannot be derived from our results. In contrast, the survival probability curve in our study shows a constant downward trend even after 27 years of exposure and the evidence strongly suggests that it will be continued until host availability has reached a value that may be critical for the survival of the pathogen.

We found significant site parameters critical for survival that were also unraveled in earlier studies such as water status. Trees growing in locations with moister growing conditions are under higher risk to die compared to those growing in drier locations. The hazard ratio suggests that trees growing at sites with excessive water status have a 1.8-fold higher risk of death compared to trees growing under sufficient water status and a 3.6-fold higher risk compared to trees growing under dry conditions. In accordance, trees growing at sites which experienced one more months with extreme rainfall surplus during the observation period had a 1.07 fold higher risk. Both covariates are likely to favour the disease, since moisture is a critical factor during infection and for the efficient spread of ascospores<sup>12</sup>. Excess moisture may also play a critical role for growth of other wood-decaying fungi such as *Armillaria spec.*, which were recently found to be involved in subsequent root rot of ash trees after infection with ADB<sup>24,28</sup>.

Aalen's additive regression model also unraveled months with extreme high temperature as well as months with extreme rainfall deficit as factors which reduce the risk of death. While this pattern is largely corroborated by other studies<sup>26</sup>, the effect sizes of both covariates in our model were only moderate and hence it deserves more investigation before concise conclusions can be drawn for those two environmental variables.

Lower host abundance was recently associated with lower mortality in Swiss ash stands<sup>19</sup>, but our study did not confirm this relationship. At continental scale ash trees were killed regardless of whether they occurred in high abundance or low abundance. This demonstrates probably once more the devastating and highly efficient spreading capacity of the pathogen which allows the fungus to enter new territory within a short time<sup>22,29</sup>.

This study shows the value of ICP Forests level I data for monitoring ash dieback at continental scale. Although *F. excelsior* and *F. angustifolia* are minor tree species in most of the survey countries, they nevertheless constitute keystone species with high importance for ecological communities and local economy<sup>4,18</sup>. In the British Isles and Ireland, the importance of ash is even higher as *F. excelsior* is occupying a larger proportion of woodlands compared to other countries<sup>30,31</sup>. Unfortunately, the United Kingdom never assessed ash for defoliation and left the ICP Forests Level I network in 2011 so that no data on ash dieback is currently available from there.

Overall our study indicates a strongly progressive pattern of ash decline across the last three decades and we estimated that an Europe-wide average defoliation of 50% could be reached as early as 2030. However, we also outlined that the disease strongly differs among regions, since the progress seems to be slower in the south compared to the north. The threshold of 50% defoliation can be seen indeed as a critical benchmark, since we estimated that trees that have reached this defoliation status died on average within the following 9 years (data not shown). A further decline without joint rescue efforts at European level could cause non-reversible loss of genetic diversity which in turn could cause a critical minimum population size vital for long-term survival. Although a minor proportion of ash trees is likely inheriting resistance against ADB<sup>32,33</sup>, this alone will not guarantee that the ash population will recover after the disease has reached an equilibrium state. Evans<sup>34</sup> simulated that long-term recovery of ash is highly dependent on the proportion of ash trees carrying natural resistance and secondly on the degree of heritability of resistance. However, even under extreme high heritability assumptions, long-term recovery under natural conditions will remain low when the founder population consists of only few trees<sup>34</sup>. Hence, without efforts at European level it is very likely that the two ash species *F. excelsior* and *F. angustifolia* will face the same fate as dutch elm (*Ulmus spec.*), which largely disappeared in most parts of Europe after the outbreak of the devastating dutch elm disease<sup>35,36</sup>. Even though our results apply mainly to ash trees located in



forests and probably exclude trees that are situated in open landscapes such as along alleys, parkways, and in yards, the urgency of the matter is nevertheless justified given that natural regeneration in forests will be driven by healthy seed trees which survive within forest sites.

Conservation efforts at national level have recently been undertaken in Great Britain, Ireland, Denmark, and Austria and new projects are currently starting in Germany and other countries. For instance, reference genomes for *F. excelsior* and *F. angustifolia* have been completely sequenced<sup>37,38</sup> and novel markers which are able to discriminate between resistant and susceptible *F. excelsior* trees have been developed<sup>39</sup>. On the other hand, progeny tests which aim to evaluate resistance against ADB of several thousand saplings of European ash harvested from field-resistant mother trees are currently being tested in Austria (<http://www.esche-in-not.at/index.php>). Constant monitoring of Ash vitality in natural forest stands but also in field trials will particularly become crucial in the future given that the invasive Emerald ash borer (*Agrilus planipennis*, EAB) is already entering European territory and constitutes a threat to European ash species in the same order of magnitude as compared to *H. Fraxineus*. Emerald ash borer is currently responsible for mass decline of ash in Russia and was recently detected not more than 100 km from the eastern border of the European Union<sup>40</sup>. In analogy to the pathosystem between asian ash species and *H. Fraxineus*, ash species such as *Fraxinus mandshurica* or *F. chinensis* have most likely co-evolved with Emerald ash borer, which probably led to high natural genetic variation in host susceptibility within these species<sup>37</sup>. While such intra-specific variation could indeed guide national and international breeding programs (e.g. in hybrid breeding or through genomic selection) careful attention needs to be paid in order to avoid maladaptation if both traits (resistance against ADB and resistance against EAB) are negatively correlated. In any of these scenarios, we strongly believe that only a pan-European initiative will be capable of utilizing the already numerous gathered resources in order to avoid ash disappearing from the European forest landscape.

## Methods

**Data.** We used the ICP Forests Level I forest damage survey since this dataset constitutes the only available systematic survey sample across Europe at a 16 × 16 km grid<sup>41</sup>. Within this dataset, crown parameters and damaging agents are assessed at an annual scale (but see exceptions in Table 1) by survey teams typically including 24 dominant trees per plot. Crown defoliation is assessed in 5%-steps with 99% indicating complete defoliation of a tree and 100% its death. Damaging agents are assessed and are divided into abiotic, biotic and other damage causes. We selected all plots where at least one ash tree (either *F. excelsior* or *F. angustifolia*) was recorded and analysed the complete survey period spanning the years 1987 to 2020. An ash tree was subsequently classified as dead when its defoliation status reached 100% and the tree did not occur any longer in subsequent survey years.

**Overall survival probability after 30 years.** Mortality data in tree ecology is often treated as a binary variable that can be best accommodated by logistic regression analysis<sup>14,42,43</sup>. However, when the cause of death is primarily caused by a pathogen which resembles a mortality pattern close to a pandemic situation (i.e. a time-to-death approach), logistic regression will be rather unsuitable. The reason for this is that the data are usually censored, which either means that at a specific survey date not all subjects had yet experienced the event (i.e. death) or got lost without any further assessments conducted<sup>44</sup>. Consequently, we used a different approach that specifically treats time-to-event data and that is usually applied in medical data such as survival analysis for patients carrying a lethal disease<sup>45,46</sup>. We justify this because of two reasons: (i) ash dieback usually constitutes a dead end for infected trees, since the disease is highly lethal and progressive and recovery of trees is rarely observed<sup>12</sup>, (ii) ash dieback spreads through windborne ascospores at a fast rate so that we can assume that a large part of the ash population in Europe has already experienced high and equal infection pressure<sup>29</sup>.

We first estimated the overall survival probability of ash with the Kaplan–Maier step function written as:

$$\hat{S}_{KM}(t) = \prod_{s < t} \frac{\bar{Y}(ts) - d(s)}{\bar{Y}(s)} \quad (1)$$

with  $S_{KM}$  being the overall survival probability,  $\bar{Y}(ts)$  being the trees at risk at time  $t$ ,  $d(s)$  being trees that died since start of infection and  $\bar{Y}(s)$  being the trees at risk since the beginning of infection. Since the observation plots are usually re-visited each year, the Kaplan–Maier curve will display the overall survival probability and 95% confidence intervals at one-year steps. We calculated the overall survival probability for two different models: (i) Model 1 with simultaneous infection: in the first model we assumed that the start of infection happened in 1992 for the entire European population. This is the first date when ash dieback was observed in Europe (Northern Poland) and it is generally believed that this is the epicentre of the disease<sup>12</sup>. (ii) Model 2 with non-simultaneous infection: although the disease spread rapidly towards the west, east, and south from the epicentre, there were distinct time gaps between subsequent infections of ash populations located further apart from the epicentre. Hence, we gathered dates of first observations of ash dieback (Table 1) for all European countries from different literature resources<sup>6,22</sup>. Even though these dates are to some extent biased and may do not reflect the exact date of arrival of ash dieback at national level, they can nevertheless serve as a good proxy for the temporal delay in infection due to expansion history of the disease. In few cases, the time between last assessment and event [nominator of Eq. (1)] was negative in the second model, since some mortality already occurred before the estimated arrival of ash dieback. This affected only Spain and southern France, where some cases of mortality were attributable to other disturbance agents rather than to ash dieback (see “Discussion” below). These few cases were consequently removed from both models.

**Cox proportional hazard model and Aalen additive regression model.** In order to model the transition from “alive” to “dead” we used a Cox-proportional hazard model<sup>47</sup> and, alternatively, an Aalen additive

regression model<sup>48</sup>. Such models are commonly applied in clinical testing for explaining mortality patterns for patients under risk when the data is right- or left-censored<sup>49</sup>. Both models are capable of incorporating covariates of different structure and specifically relate those covariates to survival patterns or any other censored outcome. The Cox-model has the form:

$$\lambda(t) = \lambda_0(t) e^{\beta_1 x_1 + \beta_2 x_2 + \dots} \quad (2)$$

where  $\lambda(t)$  is the single-tree hazard as a function of time  $t$ ,  $\lambda_0$  is the so-called baseline hazard,  $X_{1,2}$  are the covariate vectors of subject  $i$  and  $\beta_{1,2}$  specify vectors of coefficients associated with the covariates<sup>49</sup>. The Aalen additive regression model was suggested as an alternative to the Cox-proportional hazard model, because some of the assumptions behind the Cox-model may not always be met by all included covariates (e.g. that all coefficients are constant over time) and because additive effects may reflect the nature of the underlying disease better than the proportionality assumption, in particular when the baseline hazard is very small. The additive model has the linear form:

$$\lambda(t) = \beta_0(t) + \beta_1(t)x_1 + \beta_2(t)x_2 + \dots \quad (3)$$

with  $\beta_0$  being the baseline function and  $\beta_1(t)x_1$  being the regression functions which determine the influence of the covariates. In contrast to the Cox-proportional hazard model, regression functions in (3) can freely vary over time.

We used two key stand characteristics from the ICP Forests Level I dataset (water availability coded as 1 = insufficient, 2 = sufficient, 3 = excessive and humus type comprising 9 classes) as well as abundance of ash trees in each plot (number of ash trees/total number of trees) as survival predictors. The rationale behind the latter variable is that we hypothesize higher mortality rates when the host abundance is high compared to stands where only few ash trees occur.

Various recent studies showed that tree mortality, in particular in the very last years, has accelerated mainly as a result of climatically-driven changes such as warming and drought<sup>50,51</sup>. In order to disentangle whether the mortality pattern in ash between 1987 and 2020 has been driven stronger by ADB, climate or both, we calculated the monthly anomaly in maximum temperature and precipitation sums from 1995 to 2020 for all survey plots in which a few ash trees occurred. We used E-OBS daily gridded meteorological data at 0.25° spatial resolution<sup>52</sup> and calculated the number of extreme events between 1995 and 2020 for each survey plot. Extreme events were defined as months which showed a standardized climatic anomaly of  $\geq$  or  $\leq$  two standard deviations above or below long-term average, respectively.

Since we expect that some covariates are not randomly distributed in space across the observation plots (i.e. the disease is generally stronger in the east compared to the west of Europe due to the infection history), we divided the data also into geographic strata so that each group (eastern, western, southern, and northern Europe) would have its distinct baseline hazard function, but common values for  $\beta$ . We employed the *survival* package in R<sup>53</sup> for all analysis steps (overall survival probability, Cox model, Aalens additive regression model) described above.

**Time-series forecasting of crown defoliation.** Finally, we aim to project the past defoliation history (1987–2020) of ash in Europe into the near future in order to determine critical time horizons for conservation and rescue management. We first calculated average defoliation per year and plot including all ash trees and performed timeseries forecasting spanning 50 years from the last available observation (2021–2070). We used both an ARIMA (autoregressive integrated moving average) model as well as exponential smoothing (Holt's linear trend method according to Holt<sup>54</sup> as alternative approach. Briefly, a non-seasonal ARIMA model was fitted by determining the parameters  $p$ ,  $d$ , and  $q$  where  $p$  is the order of the autoregressive part,  $d$  is the degree of first differencing, and  $q$  is the order of the moving average part. We first determined the three parameters by using the *auto.arima* function on the log transformed defoliation time series with the help of the *forecast* package in R<sup>55</sup>. In order to evaluate whether the determined parameters were correctly chosen, we visually inspected the partial autocorrelation plot and checked the model residuals by performing a Portmanteau-test. We calculated 95% confidence intervals around both estimators (ARIMA, exponential smoothing) and evaluated the goodness of the obtained forecasts by using the first 22 years (1987–2009) as training dataset and the last ten years of observations (2010–2020) as evaluation data set. The mean square error (MSE) was used to compare forecast results between the two methods. Since Sweden and Norway changed their monitoring system in 2009 and 2013, respectively (see Table 1), we used only the period 1987–2010 for the northern group (see also results below).

## Data availability

This dataset will be available via Zenodo.org upon publication.

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## Author contributions

J.P.G.: Formal analysis, Methodology, Writing—original draft, Visualization, Project administration, Funding acquisition. T.S.: Resources, Writing—review & editing. V.T.: Resources, Writing—review & editing. N.P.: Resources, Writing—review & editing. M.L.: Conceptualization, Methodology, Writing—original draft, Supervision, Project administration, Funding acquisition.

## Competing interests

The authors declare no competing interests.

## Additional information

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