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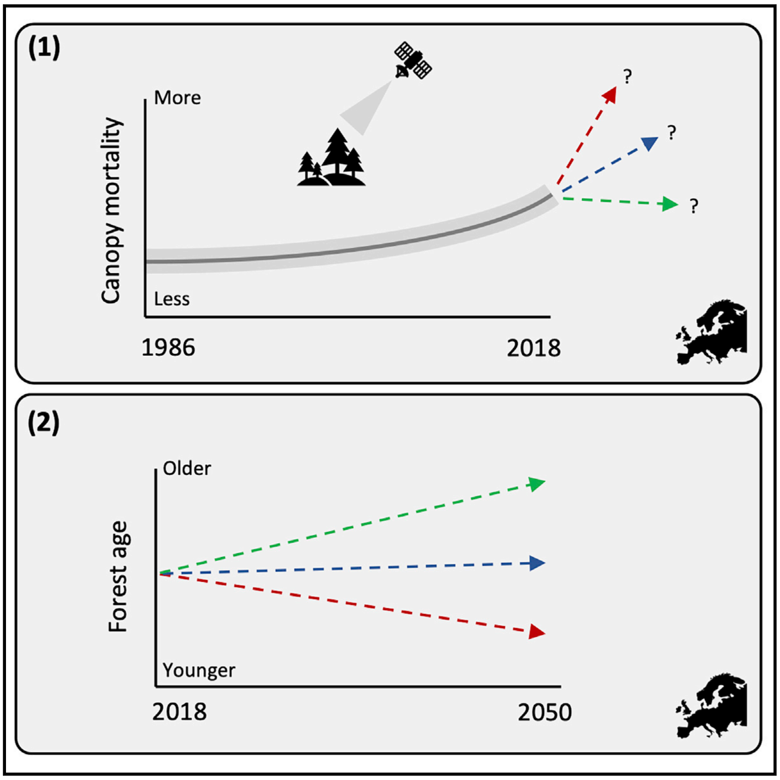
# Increasing canopy mortality affects the future demographic structure of Europe's forests

## Graphical abstract




## Highlights

- Canopy mortality has consistently increased across Europe in the past three decades
- Increasing canopy mortality will have profound changes on forest demography
- Current rates of canopy mortality hold the aging trend of Europe's forests
- Future increases might lead to widespread decline in forest age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## In brief

Land use and climate change are expected to increase tree mortality globally. Using satellite data, we show that tree mortality has increased consistently across Europe. Increasing tree mortality can affect the demography of Europe's forests, shifting them toward younger age, which has widespread ecological consequences. Increasing tree mortality should thus be a key priority for forest policy and management.


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# Increasing canopy mortality affects the future demographic structure of Europe's forests

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**SCIENCE FOR SOCIETY** Land use and climate change are challenging forests around the globe. An important indicator of increasing pressure on forest ecosystems is tree mortality, that is, the proportion of canopy trees dying per year from both natural and human causes. Increasing canopy mortality can substantially alter the demography of forests toward younger age, which can have widespread negative consequences for both forest biodiversity and carbon storage because old forests provide valuable forest habitat and have high carbon stocks. We show that canopy mortality has increased across all of Europe in the past three decades. Those increases in canopy mortality can hold the historic aging trend of Europe's forests and—if increasing further—push Europe's forests toward younger age. In order to sustain the important services provided by Europe's forests to society, developing strategies to address increasing tree mortality should be a key priority of forest policy and management.

## SUMMARY

Increasing tree mortality can have pervasive impacts on forest dynamics. Yet, large-scale trends in tree mortality and their effects on forest demography remain poorly quantified despite the important role of forest demography for forest carbon pools and biodiversity. Analyzing satellite data at 19,896 plots, we here show that canopy mortality in 35 European countries increased from 1985 to 2018 (+1.5% ± 0.28% $yr^{-1}$). Using simulations, we demonstrate that recent levels of canopy mortality will halt the aging trend of Europe's forests and that a further increase in canopy mortality has the potential to strongly alter Europe's forest demography toward younger forests. These demographic changes will have cascading negative effects on forest biodiversity and carbon storage. Developing strategies to address the increasing canopy mortality should thus be a key priority of forest policy and management in Europe.

## INTRODUCTION

Tree mortality is a key demographic process in forest ecosystems. It drives natural ecosystem dynamics and occurs at different spatial scales, from the level of individual trees[1,2] to large-scale pulses of mortality, referred to as disturbances.[3] Although many causes of tree death are natural (e.g., resource limitation, wildfire, or outbreaks of native insects), there are also human causes of tree death related to land use (e.g., societal demand for resources[4] or the introduction of alien forest pests[5]). Both natural and human causes of tree death have been found to increase across many forest ecosystem globally,[5–8] raising concerns about the potential impacts on the global forest.[9,10]

Large-scale changes in tree mortality can have substantial impacts on forest ecosystems. Trees are long-lived organisms and regenerate slowly, and an increase in tree mortality can shift the population structure of forests toward younger trees.[11] Globally, the share of young forests has already increased from 11.3% to >33.6% since 1900.[12] Such shifts in forest demography can have ripple effects on forest functions and services.[13,14] For example, old forests represent important habitat for many forest-dwelling species,[15] and the observed trend toward a younger population structure could therefore have negative impacts on overall forest biodiversity. Old forests are likewise important for carbon storage,[16,17] and a shift in forest demography toward younger forests could reduce the carbon-storage potential of forests. Given the substantial impacts of increasing

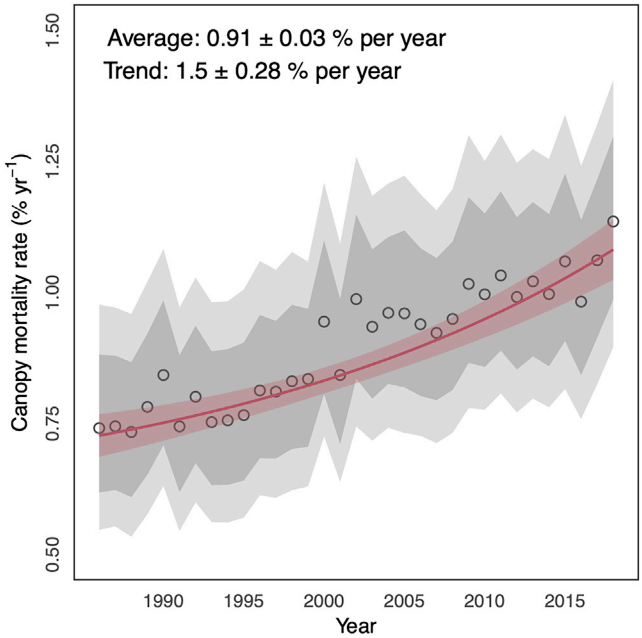


**Figure 1. Canopy mortality rates and trends in Europe's forests**
Black circles indicate the mean continental-scale canopy mortality, and gray ribbons indicate the uncertainty range (darker gray, standard deviation of the posterior distribution; lighter gray, 90% credible interval). The red line gives the mean temporal trend and its standard deviation.

tree mortality on forests demography, it is essential to monitor and understand changes in tree mortality from the individual to the continental scale.

For Europe, there is accumulating evidence that tree mortality is increasing.[8,18–20] This increase in tree mortality might be explained by an increased utilization of Europe's forest resources[20,21] as well as by more frequent and severe natural disturbances.[8,18] Both the increased utilization of Europe's forest resources and increasing natural disturbances affect forest demography and thus influence the functioning and ecosystem services of Europe's forests.[8,22–24] However, most of the evidence for increasing tree mortality in Europe relies on compilations of gray literature[8,18] or focuses on regional trends.[19,20] Thus, robust long-term trends of tree mortality and quantitative estimates of the resulting impacts on forest demography are missing. We here address these knowledge gaps by (1) manually interpreting satellite images at 19,896 plot locations covering 210 million ha of forest area and a 34-year period from 1985 to 2018 in order to robustly quantifying trends in natural and human-caused canopy mortality for continental Europe and by (2) applying simulations to determine how trends in forest canopy mortality could potentially affect the demography of Europe's forests under scenarios of stabilizing as well as further increasing canopy mortality. We find that canopy increased from 1985 to 2018 by +1.5% ± 0.28% $yr^{-1}$ and that recent increases in canopy mortality have the potential to strongly alter Europe's forest demography toward younger forests. These pervasive changes in forest dynamics can have cascading negative effects on forest biodiversity and carbon storage of Europe's forests.

## RESULTS AND DISCUSSION

### Trends in canopy mortality rates

Canopy mortality increased by 1.50% ± 0.28% per year across Europe (Figure 1). The average canopy mortality rate in the late $20^{th}$ century (1985–1999) was 0.79% ± 0.04% $yr^{-1}$ (i.e., a forest area of 1.7 million ha affected by canopy mortality each year) and increased to 0.99% ± 0.04% $yr^{-1}$ (i.e., 2.1 million ha $yr^{-1}$) in the early $21^{st}$ century (2000–2018). Mortality increased at an accelerating pace throughout the observation period, and the highest canopy mortality rate of the past 34 years was observed in 2018 (1.14% ± 0.16% $yr^{-1}$).

Changes in canopy mortality varied substantially between countries and regions (Figure 2). Of the 35 countries analyzed, 28 had a positive trend in canopy mortality (Figure 2; Table S1 and Figure S2). Trends were strongest in central and eastern Europe, where canopy mortality increased on average by 55% and 78%, respectively, from the late $20^{th}$ to the early $21^{st}$ century. Weaker but still positive trends were found for western and northern Europe, where canopy mortality increased on average by 39% and 19%, respectively, over the same period. No evidence for changes in canopy mortality was detected for southwestern Europe, and evidence for increasing canopy mortality in southeastern Europe was weak (Figure 2).

Drivers of increasing canopy mortality are manifold and interactive and vary locally. Although an in-depth analyses of these local drivers is beyond the scope of this study, we here discuss several coinciding continental-scale developments that are likely to contribute to the overall increase in canopy mortality observed for Europe: first, large parts of Europe's forests have accumulated high biomass stock over the past decades,[25] and many countries have started utilizing their growing timber resources more actively by increasing annual fellings.[26] The notion that timber harvest is an important factor contributing to increasing canopy mortality is also supported by a high correlation of our estimates with data from wood-harvesting statistics (Figures S3 and S4), indicating that the vast majority of canopy mortality detected herein is, in fact, removed from the forest for the production of timber. This does, however, include both planned harvest and salvage logging in response to natural disturbances. Second, the collapse of the Soviet Union led to large-scale transformations of economic and political systems in parts of Europe, resulting in a pronounced increase in both regular harvests and illegal logging.[27] The particularly strong increase in canopy mortality rates observed for European countries of the former Soviet Union (Figure S2) can in part be explained by those historical legacies. Third, many forests across Europe have seen episodes of large-scale storm events and severe bark beetle outbreaks in recent decades,[8] which most likely contribute to the particularly strong trends observed for central and eastern Europe. Hence, increased natural disturbances—a result of both structural legacies and climate change[28]—can thus be considered an additional important driver of increasing canopy mortality trends. Increased tree mortality caused by drought has further been reported for Europe recently,[7,29,30] and the particularly high mortality rates observed for 2018 might be a consequence of the recent drought affecting large parts of Europe.[31,32] In this context, it is interesting to note, however, that we did not find strong evidence for increasing canopy mortality in southern Europe despite the

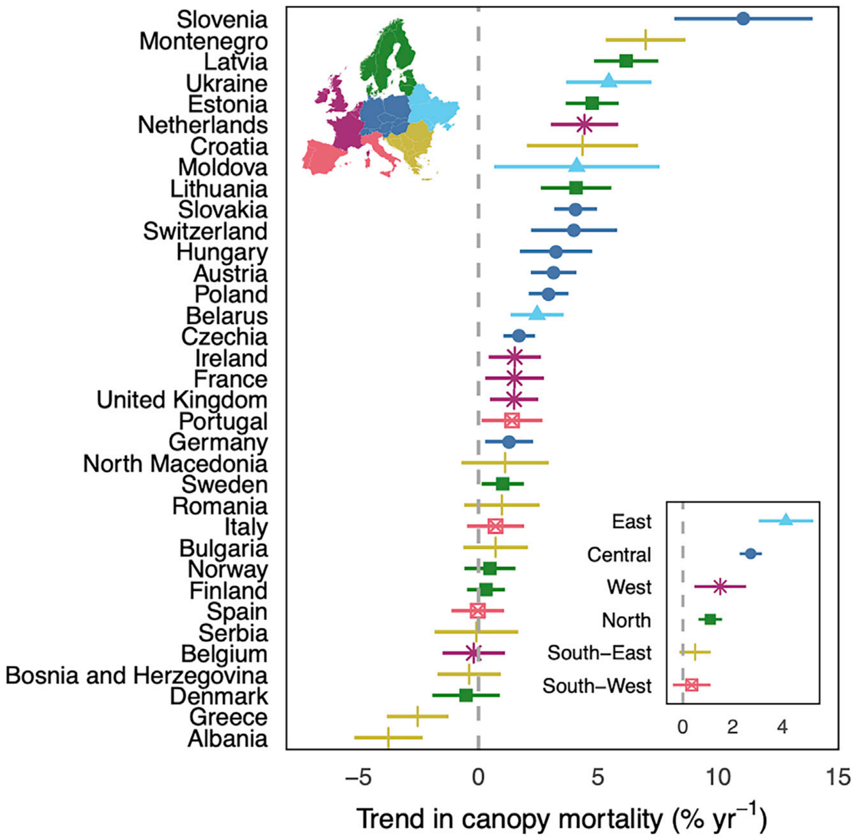


**Figure 2. Trends in canopy mortality at the country and regional levels**

Dots indicate the mean trend in canopy mortality from 1985 to 2018, and error bars give the standard deviation of the posterior distribution. Colors indicate the assignment of countries to different regions (see insets).

notion that warm and dry areas are particularly prone to drought-induced forest dieback.[7] In the past, drought-induced forest dieback in Mediterranean systems might have still been too dispersed to trigger substantial changes in canopy mortality as observed from satellite imagery.[33] Likewise, although increasing forest fire activity is expected across the Mediterranean[34] and the actual number of fires has increased in the past, the annual area burned has decreased in recent decades[35] (see also Figure S5). Despite this overall decrease in burned area across southern Europe, the years 2017 and 2018 were both characterized by unprecedentedly strong fire seasons,[36,37] which further contributed to the high mortality rates in Europe's forests in 2017 and 2018. Finally, we note that only 2.6% of the observed mortality events led to a change in land use from forest to non-forest land. That is, land-use change is of relatively minor importance for forest canopy mortality in Europe.

## Impacts of increasing mortality on forest demography

We found widely varying demographic trajectories in the three scenarios of future forest mortality in Europe (Figure S6). A stabilization of canopy mortality at the level observed in the past (1985–2018) would not result in drastic demographic changes (Figure 3). This scenario in fact increases the proportion of countries with considerable amounts of old forest (i.e., median forest age of 60 years or older) in comparison with the current situation. The aging trend currently observed in Europe's forests thus outweighs the effects of tree mortality on demography in this scenario. Canopy mortality rates at the level observed for 2018, however, stop the aging trend of Europe's forests (Figure 3), leading to an increase in countries dominated by young forests (median age younger than 30 years). A continued increase in canopy mortality at the rates observed for the past 34 years would lead to considerable shifts in the age structure of Europe's forests (Figure 3). For instance, although the forests of only 14% of European countries have a median age younger than 30 years today, this number will increase to 53% ± 3% in 2050 if observed canopy mortality trends continue. A continued increase in canopy mortality would thus inverse the current aging trend of Europe's forests.

Changes in forest demography resulting from increasing canopy mortality have the potential to challenge Europe's forests in at least three important ways. First, a shift toward younger forests will complicate the natural regeneration of forests as a result of decreasing seed availability and increasing distance to seed sources because the share of mature trees producing seeds on the landscape will decrease.[11] Second, the prevalence of old forests could be substantially reduced under a continued increase in canopy mortality. Such a shift toward younger forests simultaneously reduces the diversity in age classes on the landscape, resulting in a biological homogenization of forest habitats.[38] Given that both the prevalence of old forests and the diversity in developmental stages are important indicators of biodiversity,[39] a future increase in canopy mortality could have widespread negative consequences for forest biodiversity. Third, increasing canopy mortality reduces the residence time of carbon in forest ecosystems[40,41] and has negative impacts on the total carbon stored in forests.[42] Likewise, old forests are hotspots of forest carbon storage and act as long-term carbon sinks.[16,17] Fewer old forests as a result of further increasing canopy mortality rates would thus reduce the carbon-storage potential of Europe's forests. A continued increase in canopy mortality might hence offset enhanced carbon uptake from accelerated tree growth under climate change.[41]

## Limitations and uncertainties

We here employed remote-sensing data to obtain a consistent picture of canopy mortality rates and trends across Europe. Although remote-sensing data offer a unique opportunity to consistently estimate canopy mortality across broad spatial scales and political boundaries, they come with certain limitations that need to be considered when interpreting our results. First, we note that tree mortality is a process operating at variable scales, from single trees to entire landscapes, and because of the rather

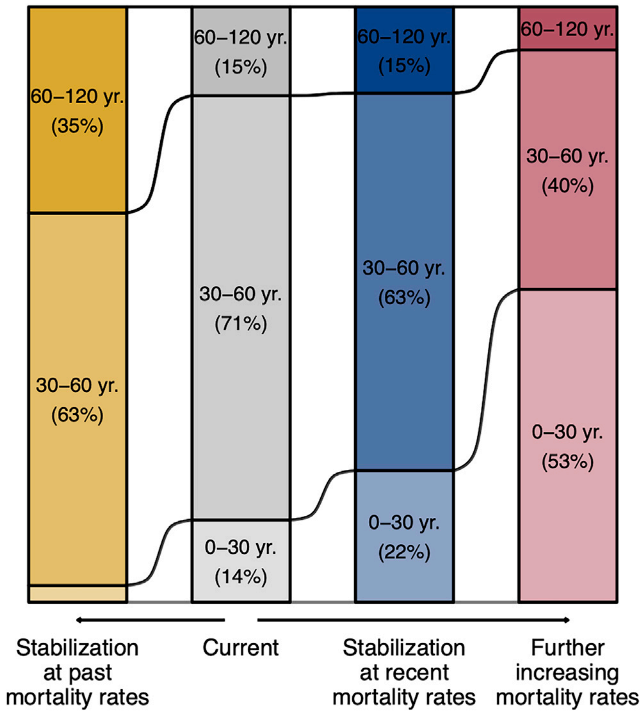


**Figure 3. Effects of changing canopy mortality rates on the median age of Europe's forests in 2050**

The distribution of median ages of the forests of 29 European countries was simulated for the year 2050 under three scenarios: (1) stabilization at canopy mortality rates observed between 1985 and 2018 ("stabilization at past rates"), (2) stabilization at canopy mortality rates observed for the year 2018 ("stabilization at recent rates"), and (3) increasing canopy mortality rates, extrapolating trends observed from 1985 to 2018 for each country ("further increasing mortality rates") (see Figure S15 for details on the three scenarios). The "current" condition shows the distribution of median ages in 2015. Percentage values show the distribution of countries in different bins of median age. We here show the averages over all landscape configurations and mortality functions, see Figure S7 for the results of individual landscape configurations and mortality functions. See Figure S6 for a detailed representation of individual runs of the NLMs for each country.

coarse spatial grain of our analysis (30 m), we omit the finest scale of tree mortality (i.e., individual tree death). Although the degree of omission is difficult to quantify, we estimate that most mortality events affecting a group of canopy trees will be recognizable in a distinct spectral change in the satellite data. That said, the mortality of individual trees, as well as mortality happening sub-canopy, will most likely be omitted in our analysis. Our estimates of mortality are thus strict canopy mortality estimates and are likely to underestimate the true rate of total tree mortality. Second, we note that because of the intensive manual interpretation, our sample sizes are limited. To account for this, we employed a set of statistical tools that prevent the detection of false positive trends arising from noise in the data (see the experimental procedures). The absence of positive trends in our analysis might thus be a result of too few data to reliably estimate an increase in canopy mortality and cannot be taken as evidence of absence of trends. We thus encourage further research to verify or improve our results. Further work should also aim to identify the underlying causes of mortality to clarify whether human or natural causes are responsible for the observed increase in canopy mortality in Europe. Finally, we note that our simple simulation-based scenario analysis of demographic changes is not meant to predict actual forest development in Europe. Uneven-aged stands, which cover approximately 28% of the European forest area,[21] are not well represented in our modeling, for instance. Future work using more elaborate simulation approaches should thus be used to investigate the patterns and consequences of changing canopy mortality rates in more detail.

## Conclusion and management implications

Here, we provide quantitative evidence that natural and human-caused canopy mortality rates have increased consistently throughout the past 34 years in Europe and that a further increase has the potential to substantially alter Europe's forest demography. It is of paramount importance for forest policy and management to carefully monitor the ongoing trends in forest mortality, better understand their underlying drivers, and implement strategies to safeguard the functions and services provided by Europe's forests. This could be achieved via (1) increasing the resistance and resilience of Europe's forests to natural disturbances by, e.g., counteracting biological and structural homogenization; (2) conserving existing and promoting future old-growth forests, especially in places where the risk of natural disturbances is low; (3) accounting for natural disturbances in long-term forest planning; and (4) considering demographic consequences of managing forests for a bio-based economy. We conclude that developing strategies to address increasing tree mortality should be a key priority of forest policy and management in Europe.

## EXPERIMENTAL PROCEDURES

### Resource availability

#### *Lead contact*

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Cornelius Senf (Cornelius.senf@tum.de).

#### *Materials availability*

This study did not generate new unique materials.

#### *Data and code availability*

All data and code for reproducing the analysis presented in this study have been deposited to Zenodo: https://doi.org/10.5281/zenodo.4682960. The satellite imagery used in this study is freely available from the United States Geological Service at https://earthexplorer.usgs.gov.

### Estimating canopy mortality rates

We used a stratified random sampling design to select plots for satellite image interpretation across continental Europe. Continental Europe here includes 35 countries (Table S8 and Figure S9) with a minimum land area of 10,000 $km^2$ (i.e., excluding Lichtenstein, Luxembourg, Monte Carlo, and Malta). A plot was defined as a 30 × 30 m square corresponding to a Landsat satellite pixel. We used an equalized stratified sampling design by randomly placing 500 plots within the forest area of each country. We used an equalized stratified sampling design over a proportional sampling design because sampling proportional to forest area would have led to sample sizes too large for manual interpretation in some countries (e.g., Finland and Sweden), whereas only a few samples would have been placed into others (e.g., Denmark and the Netherlands). We determined the sample size by balancing precision and interpretation effort by using simulation analysis to guide the decision (i.e., simulated power calculations using an assumed range of canopy mortality rates between 0.5% and 1.5% per year).[20] Forest areas were determined with a Landsat-based forest cover map created on the basis of data and methods

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presented in a previous study.[43] The resultant forest map identifies all areas that have been forested at some point in time during the study period from 1985 to 2018. Using a forest-cover map for stratifying our sampling greatly improved sampling efficiency but also led to selecting plots falsely identified as being forested. We excluded these plots during satellite image interpretation, resulting in varying realized sample sizes per country (Table S7). Data for six countries (Austria, Czechia, Germany, Poland, Slovakia, and Switzerland) were taken from a previous study,[20] which used a similar sampling design but larger sample sizes. To avoid loss of information from down-sampling, we used the full sample sizes for those countries but tested whether our results remained consistent across the pan-European dataset (see Figure S10).

For each plot, we manually interpreted temporal-spectral profiles of all satellite imagery available in the Landsat archive to assess whether a canopy mortality event occurred at this specific plot location in any given year over the time period of 1985–2018. The approach follows image processing routines and image interpretation protocols developed in a previous study,[20] and we here only give the salient details needed for understanding our approach (but see the full response design presented in the supplemental experimental procedures). A canopy mortality event was defined as any loss of canopy (e.g., biotic natural disturbance, abiotic natural disturbance, regular timber harvest, sanitation logging) that resulted in an identifiable change in the canopy's spectral reflectance properties. The interpreter thus made an informed decision on whether the spectral change was caused by a mortality event or was the result of clouds, noise, vegetation phenology, or other ephemeral changes not related to structural changes in the forest canopy. Hence, the final measurement recorded for each plot and year was the presence or absence of a canopy mortality event. The manual interpretation of temporal-spectral profiles is a well-established method[44] that yields more precise estimates of annual canopy mortality rates than automated algorithms.[45] Moreover, it allows for detecting several disturbances per plot, which is highly challenging with current automated algorithms. Manual interpretation of temporal-spectral profiles has been successfully applied across many forest ecosystems globally.[20,46–49] Yet, the final call for each plot and year remains a human decision and is thus prone to errors, similar to human measurements taken in the field. Although most mortality events will result in well-identifiable spectral changes that are easy to detect (see Figure S11 for an example), it is particularly challenging to detect low-severity mortality events that have small spectral changes in relation to the noise inherent to satellite time series. Although we cannot rule out the omission of such low-severity mortality events, we aimed to make their detection as consistent as possible: for each plot, we ran an automatic change-detection algorithm[50] and compared the outcome with our human interpretation. If there was an inconsistency between the human and automatic interpretations, the most knowledgeable interpreter revisited the plot to check whether the initial interpretation was correct. If an error was observed, we corrected the initial interpretation. Although this procedure is not able to rule out all potential measurement errors, it guarantees a high degree of consistency in the assessment because plots that were particularly hard to interpret were collectively interpreted by the same interpreter.

From the number of plots experiencing canopy mortality, we estimated annual canopy mortality rates by using a Bayesian partially pooled binomial model with a logit link function[20] implemented in Stan.[51] In essence, the model estimates the annual rate of plots experiencing a mortality event over the total number of plots per country by using repeated binary trials (hence the binomial likelihood function). The model estimates the proportion of the total forest area experiencing canopy mortality (at a grain of 30 m), which we here define as the canopy mortality rate. The model includes a linear regression term with the year as a predictor, explicitly modeling the fractional change (through the logit link) in the mean canopy mortality rate over time (i.e., the temporal trend in canopy mortality). The partial pooling applied to our model assumes each year's mortality rate to emerge from the same underlying distribution, which is beneficial when estimating rates in repeated measurements because it shrinks individual estimates toward the mean.[52] This shrinkage toward the mean will prevent large outliers (e.g., a year with very high mortality due to a storm or an extraordinary fire season) to dominate the trend and also reduces the impact of potential outliers related to interpretation errors on the overall result. We demonstrate the robustness of our model to omitted disturbances in a sensitivity analysis presented in Figures S12 and S13. To derive estimates at the country, regional, and continental scales, we first modeled annual canopy mortality rates and trends at the country level and then subsequently aggregated to regions (central, eastern, northern, southeaster, southern, and western Europe; Figure S8) and the continental level by using forest cover as weight (i.e., accounting for the stratified sampling design; Table S1).

### Simulating future forest demography

We used neutral landscape models (NLMs) to assess the impact of different future mortality trajectories on forest demography. An NLM constitutes a minimal model with regard to the underlying assumptions about the processes that drive landscapes. Yet they have proven to be powerful tools for assessing critical thresholds in landscape properties (e.g., the occurrence of old forests[53]). Because our aim was to determine how trends in forest canopy mortality could affect forest demography, NLMs provide a robust and parsimonious approach. We built NLMs with two different landscape configurations (random and clumped forest distribution) for each country by using the NLRM package[54] in R. The grain of the simulation was set to 1 ha (i.e., 100 × 100 m), which is close to the median patch size of natural mortality in temperate Europe.[19] For each cell, only the age of the dominant tree cohort was considered, and within-cell variation in tree age was disregarded. The extent of the simulations was fixed at 100 $km^2$ (i.e., 10 × 10 km), resulting in 10,000 potentially forested cells (hereafter referred to as "stands") simulated per country. The proportion of forested stands was set to the average forest proportion of each country. We mapped forest age classes for the year 2015 to stands on the basis of harmonized age-class distributions derived from national forest inventories of Europe[55] and large-scale scenario modeling.[8,56] The age-class distributions were given as a proportion of the forest area in 20-year bins from 0 to 160 years. For six countries (Bosnia and Herzegovina, Greece, Serbia, Montenegro, Northern Macedonia, and Moldova), age-class data were not available, which limited the simulation-based analyses to 29 countries.

After initializing the landscapes, we iteratively updated the age of each stand on a yearly basis (i.e., aging them by 1 year) over the period of 2019–2050. The annual proportion of pixels experiencing mortality was drawn each year from the Bayesian partially pooled model calibrated from observed canopy mortalities (described in the previous section). We hence used an empirical mortality model calibrated from observed data to simulate mortality rates for each country. To allocate mortality in space, we ranked each stand's likelihood of being affected by mortality according to four alternative age-based mortality functions (Figure S14). Individual tree mortality is U shaped over stand age with high mortality risk in young trees (competition for resources and self-thinning) and old trees (hydraulic limitations, disturbances such as wind and insects, and timber harvesting). Because tree mortality from competition between individual trees does not leave a strong signature in the forest canopy and is thus unlikely to be detected in our satellite-based approach to identifying canopy mortality at a grain of 30 × 30 m, we focused on the latter (i.e., the right half of the U-shaped mortality pattern over age, representing mortality of old trees) in our simulations. Specifically, we simulated a monotonically increasing canopy mortality probability with age in our NLMs (Figure S14). Furthermore, we assumed zero recovery failure in our simulations, meaning that all stands regrew after a mortality event.

We used NLMs to study three scenarios: (1) a stabilization of canopy mortality rates at the mean value observed for the period of 1985–2018, (2) a stabilization of canopy mortality rates at values observed for 2018, and (3) a further increase in canopy mortality following the country-specific trends observed for the past 34 years (see Figure S15). In total, we ran eight alternative NLM configurations per country (two landscape configurations × four alternative mortality functions) for three scenarios, which were replicated 15 times for each of the 29 countries, resulting in the analysis of 10,440 NLMs. From those NLMs, we derived the median age of forests within each country for the year 2050 as an indicator of changes in forest demography in response to the different mortality scenarios.

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2021.04.008.

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## AUTHOR CONTRIBUTIONS

C.S. and R.S. acquired the funding for the research project. C.S. and R.S. conceptualized the research project. C.S. and J.S. administrated the research project and curated the data acquisition. C.S. conducted the formal data analysis. C.S. wrote the original draft with review and editing from J.S. and R.S.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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