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Climate variability drives recent tree mortality in Europe

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Abstract

Tree mortality is an important process in forest ecosystems, frequently hypothesized to be highly climate sensitive. Yet, tree death remains one of the least understood processes of forest dynamics. Recently, changes in tree mortality have been observed in forests around the globe, which could profoundly affect ecosystem functioning and services provisioning to society. We describe continental-scale patterns of recent tree mortality from the only consistent pan-European forest monitoring network, identifying recent mortality hotspots in southern and northern Europe. Analyzing 925,462 annual observations of 235,895 trees between 2000 and 2012, we determine the influence of climate variability and tree age on interannual variation in tree mortality using Cox proportional hazard models. Warm summers as well as high seasonal variability in precipitation increased the likelihood of tree death. However, our data also suggest that reduced cold-induced mortality could compensate increased mortality related to peak temperatures in a warming climate. Besides climate variability, age was an important driver of tree mortality, with individual mortality probability decreasing with age over the first century of a tree's life. A considerable portion of the observed variation in tree mortality could be explained by satellite-derived net primary productivity, suggesting that widely available remote sensing products can be used as an early warning indicator of widespread tree mortality. Our findings advance the understanding of patterns of large-scale tree mortality by demonstrating the influence of seasonal and diurnal climate variation, and highlight the potential of state-of-the-art remote sensing to anticipate an increased likelihood of tree mortality in space and time.

Keywords

climate extremes; disturbance; early warning; forest decline; forest dieback; net primary production; remote sensing

1 Introduction

Climate change strongly influences vegetation structure and composition (IPCC, 2013). Vegetation changes in response to the ongoing warming are already evident at the global

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scale (Walther et al., 2002). Drastic shifts in the potential range of species are expected for the coming decades (Kelly & Goulden, 2008; Meier, Lischke, Schmatz, & Zimmermann, 2012). For long-lived organisms such as trees, the pace and magnitude of the expected climatic changes will likely exceed maximum migration rates and individual adaptive capacity (Meier et al., 2012). Consequently, the ecological reorganization resulting from anthropogenic climate change will likely lead to dieback of current forests, which may be followed by the establishment of species better adapted to future climate conditions.

Recently, widespread tree mortality has been observed in forests around the globe (van Mantgem et al., 2009; Peng et al., 2011; Westerling, Hidalgo, Cayan, & Swetnam, 2006; Williams et al., 2012). Changes in tree mortality can challenge the sustainable provisioning of ecosystem services to society (Cardinale et al., 2012; Thom & Seidl, 2016). Pulses of mortality alter forest structure and composition, which can induce negative climate feedbacks through adversely affecting the ecosystem carbon balance (Seidl, Schelhaas, Rammer, & Verkerk, 2014; Zhao & Running, 2010). Elevated tree mortality may also affect the provisioning of clean water (Clow, Rhoades, Briggs, Caldwell, & Lewis, 2011), timber (Allen et al., 2010), and the protection against natural hazards (Thom & Seidl, 2016). In addition, changes in tree mortality could lead to irreversible changes in forest communities by exceeding ecological thresholds (Hirota, Holmgren, Van, & Scheffer, 2011; Scheffer, Hirota, Holmgren, Van Nes, & Chapin, 2012). It is thus important to better understand the climatic drivers of tree mortality at large spatial scales, and to develop approaches that allow management to anticipate impending mortality changes.

While environmental changes (IPCC, 2013; Walther et al., 2002) are frequently invoked as main drivers of recent tree mortality (Muller-Landau et al., 2006; Williams et al., 2012), mortality remains less understood than other key ecosystem processes such as productivity (Pretzsch, 2010). Important causes of tree mortality are competition for limited resources such as light, water and nutrients (Muller-Landau et al., 2006), as well as disturbances such as wildfire and insect outbreaks (van Mantgem et al., 2009; Westerling et al., 2006). Resource availability and disturbances are highly climate sensitive processes. Consequently, climate change is expected to affect tree mortality, for example, through increased water stress (Peng et al., 2011; Williams et al., 2012), elevated wildfire activity and more severe insect outbreaks (Westerling et al., 2006; Williams et al., 2012). Climate variability and extremes as well as disturbances can be summarized as fast variables (Carpenter & Turner, 2000; Manion, 1991; Thom, Seidl, Steyrer, Krehan, & Formayer, 2013), that is, affecting ecosystems abruptly over short periods of time (from a few hours to years) (Thom et al., 2013; Williams et al., 2012).

Tree mortality is also influenced by slow variables which change only gradually (Carpenter & Turner, 2000; Manion, 1991; Thom et al., 2013). Site factors such as soil fertility and average climatic conditions have a distinct influence on tree mortality, but vary little from year to year. Tree mortality is generally high under harsh conditions, but also a favorable environment increases the probability for individual tree death, as higher growth rates intensify the competition for light, and increase the propensity for natural disturbances such as windthrow (Buma & Wessman, 2011; Stephenson et al., 2011). Tree mortality is further influenced by tree size and tree age (van Mantgem et al., 2009; Peng et al., 2011). Often tree

mortality exhibits a U-shaped, bimodal distribution with age, indicating high mortality in young trees (mainly due to competition and resource limitation) as well as old trees (decreasing physiological efficacy combined with an increasing propensity for being affected by damaging agents (Monserud & Sterba, 1999; Thurnher, Astrup, Sjølie, & Hasenauer, 2016). Both tree age and successional changes in the tree species composition affect tree mortality, but are likewise slow variables that only gradually change over time.

Considering both fast and slow variables has remained a challenge for studying tree mortality over large spatial scales. Detailed annual census data of tree survival are a prerequisite for linking tree death to fast variables such as inter- and intrain-annual climate fluctuation and weather extremes. Yet, such data are usually only available for intensively studied long-term research sites (van Mantgem et al., 2009; Peng et al., 2011), which do not allow the deduction of consistent large-scale patterns. Forest inventory data, on the other hand, can provide mortality information over large spatial scales (Hember, Kurz, & Coops, 2017; Nothdurft, Wolf, Ringeler, Böhner, & Saborowski, 2012). However, due to their five to ten year inventory cycles, their inferential potential with regard to mortality responses to climate variability and weather extremes is limited (Hember et al., 2017; Tomppo, Gschwantner, Lawrence, & McRoberts, 2010). These data limitations have hitherto constrained the emergence of a synthetic understanding of mortality patterns at large spatial scales.

Here we describe continental scale patterns of recent tree mortality using annual assessments of tree survival on monitoring plots systematically distributed throughout Europe on a 16×16 km grid (Eichhorn et al., 2016). We determined the influence of fast and slow drivers on interannual variation in tree mortality using Cox proportional hazard models (Cox, 1972). We hypothesized that the propensity of tree death increases with increasing climatic variability and extremes (fast variables). Furthermore, regarding spatial mortality patterns we expected that trees growing under harsh environmental conditions or at ecotones show elevated mortality. Finally, we hypothesized that individual tree mortality decreases with age (slow variable) in the first decades of a trees life.

In order to respond to mortality changes in ecosystem management the ability to anticipate mortality episodes in space and time is of crucial importance. In this context, the importance of early warning indicators is increasingly recognized (Dakos et al., 2008; Scheffer et al., 2012). Yet, currently no easily available and widely applicable tools for early warning against impending episodes of tree mortality are available. As tree vigor is strongly related to a tree's carbon balance and net primary productivity can be sensed remotely, we hypothesized that satellite-derived net primary productivity can serve as an early warning indicator of tree mortality (Dakos et al., 2008; Gillner, Rüger, Roloff, & Berger, 2013; Hember et al., 2017). If feasible, such an approach could be used to provide consistent hazard maps at continental to global scales (Zhao & Running, 2010), and help ecosystem management to cope with changing tree mortality (Peng et al., 2011; Scheffer et al., 2012; Williams et al., 2012).

In summary, the specific objectives of our study were (i) to describe the spatial patterns of recent tree mortality in Europe using empirical mortality information based on systematic

annual surveys, (ii) to analyze the influence of climate variability and tree age on the interannual variation in mortality, and (iii) to assess the potential of remotely sensed net primary productivity as early warning indicator of mortality.

2 Materials and Methods

2.1 Tree mortality information

Pan-European tree mortality was investigated using data from the ongoing ICP Forests Level 1 forest damage survey, which was started in 1995 and conducts annual assessments at a 16 × 16 km grid across the continent (Carnicer et al., 2011; Eichhorn et al., 2016). Typically, at least 20 dominant trees per plot with a height of >0.6 m are surveyed annually, and tree vigor and defoliation status are assessed. Damaging agents are recorded by field crews if possible, and were aggregated into abiotic, biotic and other agents for this analysis. A tree was considered dead if defoliation was 100% and the respective tree was no longer included in the assessment in the following year. We analyzed data of 13,630 plots recorded in the years 2000 to 2012, of which 2,435 plots exhibited tree mortality during this period. In total, we studied 235,895 trees, whereof 5,467 died during our 13-year study period, resulting in a total of 925,462 observations (trees × years) available for analysis (please note that not all plots were revisited every year). We started our investigation by analyzing spatial patterns of recent tree mortality across Europe, computing annual mortality rates at the plot level (i.e., the percentage of trees that died on average per year and plot between 2000 and 2012). Next, we examined the variation in mortality rate in space, and analyzed its covariation with tree age, species group, and ecoregion.

2.2 Drivers of tree mortality

We subsequently investigated drivers of mortality at the level of individual trees and years by fitting Cox proportional hazards models (Cox, 1972) (henceforth in short referred to as Cox models) using the “SURVIVAL” package in R, and multithreading the calculations with the R package “GLMULTI” (Calcagno & de Mazancourt, 2010; Therneau, 2015). Cox models are able to accommodate the right-censored data structure that is inherent to survival data (Fox & Weisberg, 2011), and are frequently applied to determine the effect of covariates in mortality studies and survival analysis, for example, in medicine (Bender, Augustin, & Blettner, 2005). They assess how a set of covariates modify a baseline hazard function, and are thus semiparametric (Cox, 1972).

For our analysis, fast variables were defined as those varying at the inter- or intra-annual level, while variables changing only at decadal scales were considered to be slow variables (and held constant over our 13-year study period). With regard to fast variables we focused on the effect of climate variability on the interannual variation in tree mortality. As important slow variable tree age was included as covariate, controlling for changing mortality rates with stand development (van Mantgem et al., 2009; Peng et al., 2011).

The influence of temperature was addressed via minimum and maximum temperature, as extremes are more important for tree mortality than mean values (Allen et al., 2010; Peng et al., 2011). We used seasonal aggregates (spring: March–May, summer: June–August, fall:

September–November, winter: December–February) to describe climate variability, here calculated by subtracting the long-term mean from the values of individual years. Likewise, we calculated the anomaly of seasonal precipitation sums to capture variation in plant water supply. These three variables we considered over the six consecutive seasons prior to the record of a tree's status, from the previous spring to the current summer (excluding current fall and winter as trees are assessed during the summer season of the current year), resulting in a total of 18 potential predictors of mortality within the Cox model framework. All climate data were at 1 km horizontal resolution, downscaled from E-OBS data with WorldClim information (Moreno & Hasenauer, 2016). Besides climate, competition for resources and social status are other important causes of mortality in forest trees (Muller-Landau et al., 2006). However competition-related predictors were excluded here, as all analyzed individuals were dominant or codominant trees (Eichhorn et al., 2016).

Akaike's Information Criterion (AIC) (Burnham & Anderson, 2004) was used to determine the model best supported by mortality observations. We derived the AIC for models containing all possible combinations of the 19 potential predictors (Table S4), and ranked them by increasing AIC (Table S5). The model most strongly supported by data was determined by the lowest AIC value (AIC_{min}), and models with a $\Delta\text{AIC} = \text{AIC} - \text{AIC}_{\text{min}}$ of <2 were reported as plausible. The model weight w_i (i.e., the weight of evidence in favor of model i being the actual best model) was determined by dividing the likelihood of the i th model, $\exp(-0.5 \times \text{AIC}_i)$, by the sum of all likelihoods. The relative importance of each predictor was evaluated by summing w_i across all the models in the full set in which the respective predictor occurred ($\sum w_i$) (Burnham & Anderson, 2004). We computed concordance, that is, the agreement of observations with predictions for two randomly chosen data points (Newson, 2010), as a measure of goodness-of-fit. A Concordance value of 0.5 indicates that half of the predictions of tree survival are correct. Regional differences in drivers of mortality were analyzed by repeating the continental scale Cox model analysis also at the level of five different ecoregions, investigating for the contingent effect of different site conditions on the impact of climate variability (Tables S6–S10; Figs S7–S21). Throughout the text we present the impact of the analyzed drivers on relative hazard of tree death, that is, the ratio of the predicted hazard under given conditions (e.g., temperature anomaly) to the baseline hazard (Gail, 2005; Therneau, 2015). To illustrate the effect of climate variation on the relative hazard of tree death we report on the sensitivities of individual drivers by changing selected covariates of interest by a fixed amount (i.e., $+2^\circ\text{C}$ for temperature, -100 mm for precipitation) while keeping the remaining covariates constant.

2.3 Remote sensing for early warning

We tested if a widely available satellite-based indicator of vegetation productivity can be used as an early warning indicator of tree mortality (Dakos et al., 2008). Specifically, we used annual net primary production (NPP) derived from the MOD17 algorithm (Zhao & Running, 2010) using daily European climate data (Moreno & Hasenauer, 2016) at 1 km horizontal resolution (Neumann et al., 2016). Consistent with the analysis of climatic drivers and tree age we built models containing both fast and slow variables. Mean NPP between 2000 and 2012 represented a potential “slow” driver of mortality, characterizing differences

in site-specific productivity levels and indicating spatially varying levels of site carrying capacity. This potential explanatory variable thus accounts for the fact that mortality is frequently reported to differ with site quality and growth rate (van Mantgem et al., 2009; Williams et al., 2012). Furthermore, we used the NPP trend prior to a mortality event as a potential fast explanatory variable. This follows the findings of previous studies that a decrease in growth can signify an impending increase in mortality (Camarero, Gazol, Sanguñesa-Barreda, Oliva, & Vicente-Serrano, 2015; Gillner et al., 2013). Three alternative trend periods accounting for the NPP development of up to two years prior to the mortality event were tested ($t-t_1$, t_1-t_2 , $t-t_2$), and the same modeling framework and variable selection approach was employed as used to study the effect of climate variability and age. The variable combination most strongly supported by the data (determined via AIC) was explored by comparing the predicted interannual variation in relative mortality hazard to the observed data. We were particularly interested if the early warning model was able to detect increasing and decreasing temporal trends in mortality (Fig. S25), which we evaluated using Gleichläufigkeit, that is, the agreement of the observed and predicted time series in their consecutive biennial trend periods (Schweingruber, 1983). For instance, a Gleichläufigkeit of 50% means that in half of the cases the observed year-to-year trend was captured satisfactorily by the model. The predicted relative mortality hazard was subsequently explored by results across Europe (Fig. S26).

All statistical analyses and visualizations were performed using the R language and environment for statistical computing (R Development Core Team, 2016). The raw mortality data used in this work are provided via a publicly accessible data repository at https://figshare.com/articles/European_tree_mortality_information/4810804 (Neumann, Mues, Moreno, Hasenauer, & Seidl, 2017). The seasonal climate data used are available from <ftp://palantir.boku.ac.at/Public/ClimateData/SeasonalAvgs/>. Furthermore, net primary production data can be obtained at ftp://palantir.boku.ac.at/Public/MODIS_EURO/.

3 Results

3.1 Patterns of recent tree mortality in Europe

We obtained mortality information from annual surveys on 235,895 trees distributed across 13,630 plots in 31 countries of Europe, representing a forest area of 177.7 million ha (Forest Europe, 2015). Out of this population, 5,467 trees died between 2000 and 2012. Patterns in tree mortality varied distinctly across Europe, with mortality hotspots on the Iberian Peninsula, in south-eastern Europe, and parts of northern Europe (Figure 1). In Central Europe, mortality rates were distinctly lower and more evenly distributed in space. The share of monitoring plots with at least one tree dying between 2000 and 2012 increased from north to south and from east to west across Europe. Mean annual mortality rate (the average percentage of trees dying per year across all plots) was 0.50% per year in Europe's forests, ranging from 1.39% per year in south-western Europe to 0.31% per year in central-western Europe (Tables 1 and S1, Fig. S1).

Tree age is an important slow driver of tree mortality (van Mantgem et al., 2009; Peng et al., 2011), and mortality rates in Europe generally decreased with age over the first 120 years of stand development. For trees younger than 20 years, mortality rates were more than doubled

compared to trees that were 100 years older (average mortality rates of 0.82% per year and 0.40% per year, respectively) (Tables 1 and S2). Uneven-aged forests had a somewhat higher mortality rate (0.69% per year) than the average over all seven age classes of even-aged forests (0.50% per year). Also life history strategy affected mortality, with light-demanding, early seral species experiencing substantially higher mortality rates (e.g., 0.80% per year for broadleaved pioneer species such as *Betula pendula/B. pubescens*) than shade-tolerant, late seral species (0.41% per year for shade-tolerant broadleaved species such as *Fagus sylvatica*; Table S3).

Biotic and abiotic causes of tree mortality occurred with similar frequency across Europe between 2000 and 2012 (Table S1). Yet, for a large portion of mortality incidents (71.4%) it was not possible to unequivocally determine the cause of tree death (Tables S1–S3), which is why we refrained from further analyses at the level of mortality agents. Furthermore, in the large majority of Europe's forests, management can mask natural mortality processes, for example, by removing defoliated trees or alleviating resource competition through thinning of suppressed trees before they die naturally (Forest Europe, 2015). Consequently, natural and anthropogenic mortality causes cannot be cleanly separated in coupled human and natural systems (Liu et al., 2007) such as Europe's forests. We thus analyzed all mortality causes jointly in the remainder of this work.

3.2 Climate variation and tree age as drivers of mortality

We found that climate variation (i.e., the deviations of temperature and precipitation from their long-term mean values) in both the current and preceding years influences tree mortality (Table S5). Both maximum and minimum temperatures significantly modify mortality, with extreme cold and hot conditions both increasing the propensity of tree death (Figure 2). Our sensitivity tests show that an increase in the summer maximum temperature by +2°C in the preceding year increases mortality of individual trees by +17.8% in the following year. Conversely, the same increase in winter minimum temperature reduces mortality by –22.9%. In both winter and summer, minimum temperature has a stronger effect than maximum temperature. Consequently, if both maximum and minimum summer temperature would increase consistently by +2°C, mortality would be reduced by –10.0%. For the same increase in extreme winter temperatures mortality would decrease by –10.4%. In a warming climate, elevated mortality related to peak temperatures could thus be compensated by reduced cold-induced mortality.

Elevated precipitation in the spring of the current year reduces the probability of mortality, while higher than average summer precipitation in the previous year increases mortality (Figure 2). Seasonal fluctuation in precipitation can thus have important yet divergent effects on the propensity of tree death. For example, reduced current year spring precipitation increases mortality (+24.6% for –100 mm in precipitation), while a reduced summer precipitation in the previous year lowers mortality (–20.9% for the same amount of precipitation change). Consequently, our data suggest that the effect of a reduction in precipitation depends on the season it occurs in. Consistent with the descriptive analysis indicating an effect of tree age on average mortality, tree age was also negatively related to mortality when the effects of climate variability were accounted in the frame of the Cox

proportional hazard models (Tables 1 and S1; Fig. S22). Under average climatic conditions an increase of tree age by 20 years from 50 to 70 years would decrease the mortality hazard of an individual tree by −25.8%.

The relative variable importance of predictors differed between ecoregions. For example, in northern Europe the effects of maximum and minimum winter temperature have a stronger influence on mortality than in the continental scale analysis, while in central Europe temperatures in spring and fall are also important (see Tables S5–S10; Figs S5–S22 for details).

3.3 Net primary productivity as early warning indicator

Growth rates and changes therein are often linked with tree mortality (Camarero et al., 2015; Muller-Landau et al., 2006; Williams et al., 2012). We thus tested whether remotely sensed net primary productivity (NPP) at 1 km resolution (Neumann et al., 2016) is able to detect spatio-temporal differences in mortality hazard across Europe's forests. The model best supported by the data includes mean NPP (an indicator of the site carrying capacity, and positively related to mortality) and NPP change in the two preceding years (indicating recent trends in resource availability and use, and negatively related to mortality) as predictors (Figure 3). A doubling in mean NPP from $350 \text{ g C m}^{-2} \text{ year}^{-1}$ to $700 \text{ g C m}^{-2} \text{ year}^{-1}$ increases mortality by 62.8%. Furthermore, for a mean productivity level of $500 \text{ g C m}^{-2} \text{ year}^{-1}$, a drop in NPP by 50% in the previous two years increases mortality by 51.9%. The predictive power of remotely sensed NPP was lower than that of age and climate variables (concordance values of 0.55 and 0.65, respectively; Figure 2; Tables S5–S12). Nonetheless, the interannual variation of tree mortality at the continental scale was correctly predicted by remotely sensed NPP in 70.0% of all years between 2000 and 2012 (Fig. S25). Based on satellite-derived NPP indicators pan-European early warning maps of tree mortality can be produced (Fig. S26).

4 Discussion

Our analysis of 235,895 trees systematically sampled across the entire European continent showed that recent tree mortality in Europe's forests is substantially driven by climate variability. This result is well in line with previous studies at smaller scales (Allen et al., 2010; van Mantgem et al., 2009; Neuner & Knoke, 2017; Neuner et al., 2015; Peng et al., 2011), and identifies inter- and intra-annual fluctuation in climate variables as well as climatic extremes as a central driver of variability in tree mortality at continental scale. Our results also revealed that the influence of climate variability on mortality is more complex than a simple monotonic relationship with temperature (Adams et al., 2009): For instance, increasing maximum temperatures during summer months could increase mortality, while similar increases in winter minimum temperatures could foster tree survival (Figure 2). In recent years, winters warmed significantly stronger than summers, particularly in the high latitudes of Europe (Luterbacher, Dietrich, Xoplaki, Grosjean, & Wanner, 2004), suggesting that the net effect of warming might be reduced tree mortality in these areas. Overall, our continental-scale data suggest that an equal increase in maximum and minimum temperature would result in lower tree mortality in Europe. Conversely, the scenario with the worst

impact on tree mortality would be intensification in both temperature extremes (lower minimum temperatures and higher maximum temperatures in both winter and summer). With regard to water availability our results suggest that the most detrimental precipitation patterns for tree mortality are wetter than average summers followed by drier than average springs (Figure 2). Consequently, our data suggest that seasonal fluctuation in precipitation patterns (Frei, Schöll, Fukutome, Schmidli, & Vidale, 2006) might be more detrimental than unidirectional changes in the precipitation level at the continental scale. However, considerable variation in the importance and directionality of climatic drivers among ecoregions is evident (Figs S9–S13), and suggests that the local context is important for quantifying drivers of mortality.

Lower and higher latitudes of Europe exhibited higher tree mortality compared to central Europe in recent years (Table 1; Figure 1). This general pattern supports the notion that vegetation might be most sensitive to climatic changes in areas that are already experiencing harsh climatic conditions (Risser, 1995; Scheffer et al., 2012). Yet, due to our relatively short observation period, we were not able to examine temporal mortality trends and attribute tree mortality to ongoing climatic changes (Seidl, Schelhaas, & Lexer, 2011). As the monitoring underlying the current dataset is still ongoing (Eichhorn et al., 2016), we are confident that future work will be able to additionally consider the effect of changes in long-term climatic average (i.e., slow climatic variables) on tree death. A further focus of future efforts could be to more explicitly address the role of very short (i.e., 5–15 days) extreme events on tree mortality (Frank et al., 2015; Teuling et al., 2010). A more general limitation of our analysis lies in the fact that tree mortality is a highly stochastic process (Allen et al., 2010; van Mantgem et al., 2009; Peng et al., 2011). This makes it difficult to conclusively identify the causes of tree mortality in the field (Tables S1–S3), and inhibits a more process-oriented analysis at the continental scale. The fact that tree mortality often results from several agents or processes acting in combination is additionally complicating the attribution of mortality causes. Consequently, the climatic drivers of mortality identified here have to be seen as indicating conditions that decrease tree vigor and increase susceptibility to disturbance agents, but are not necessarily the root causes of tree mortality (Manion, 1991). Another important caveat of our data is that it only includes dominant and codominant trees. Notwithstanding the fact that this is the economically and ecologically most important cohort in a forest ecosystem, our mortality rates likely underestimate total tree mortality in Europe's forests.

In addition to fast variables such as climatic variability and extremes we found that also slow variables such as tree age and life history strategy were related to mortality. Over the last decades, the age of Europe's forests has decreased (Vilén et al., 2012), which – based on our analysis – can be expected to increase the mortality propensity of individual trees. More broadly, Europe's forests are intensively managed for a variety of ecosystem services (Forest Europe, 2015), thus thinning and harvesting trees are important causes of tree mortality in Europe. Nonetheless, in our analysis, ecological predictors such as climate and age were able to satisfactorily describe continental-scale mortality patterns. This seemingly paradoxical finding can be explained by the fact that management removals are often triggered by natural causes, for example, stressed trees affected by competition or pathogens are removed by management before dying naturally due to resource limitation. We thus

conclude that an analysis of climatic drivers of mortality is also meaningful for coupled human and natural systems such as Europe's forests (Liu et al., 2007). Note that we here focused on natural drivers of tree mortality. A large portion of the variation remaining unexplained in our analysis is likely related to social and economic factors influencing management decisions and subsequently tree mortality (Cardille, Ventura, & Turner, 2001; Carpenter & Gunderson, 2001).

Tree mortality is an important demographic process in forest ecosystems. As large pulses of mortality can have significant effects on the provisioning of ecosystem services and the conservation of biological diversity (Cardinale et al., 2012), early warning indicators predicting impending mortality events are important for ecosystem management (Carpenter & Gunderson, 2001; Dakos et al., 2008). Here we show that remotely sensed NPP is able to detect spatio-temporal variation in tree mortality at the continental scale (Fig. S25). As our empirical analysis indicated a high relevance of climatic parameters we employed MOD17 NPP, which integrates reflectance signals with climate data in a modeling framework based on fundamental principles of plant physiology (Running et al., 2004), rather than using purely reflectance-based indices such as the Normalized Difference Vegetation Index (Breshears et al., 2005; Verbesselt, Robinson, Stone, & Culvenor, 2009). The good results obtained with MOD17 NPP support this decision, and are particularly noteworthy as there is a spatial mismatch between the remotely sensed data (1 km horizontal resolution) and the mortality data used in this study (individual tree level). While our model is not able to explicitly capture local abiotic mortality events such as windstorms or wildfires (Figs S2-S4), it was well able to reproduce large-scale interannual mortality patterns (Fig. S25). The data needed to implement our early warning approach are readily available at large scales, which allows for a near real-time risk assessment for areas where tree loss would compromise desired ecosystem functions (Fig. S26).

Supporting Information

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Patterns of tree mortality in Europe 2000–2012. The main panel shows mortality rate (i.e., the average percentage of trees dying per year) at the level of forest monitoring plots. Please note that the color ramp is truncated to enhance readability. Marginal histograms indicate the share of plots experiencing tree mortality (i.e., the percentage of plots with at least one tree dying over the 13-year observation period) in latitudinal and longitudinal bands, respectively

Figure 2.

Climatic drivers of recent tree mortality in Europe. Shown is the relative hazard (i.e., relative change in mortality) for the two most influential seasons of maximum temperature (left column), minimum temperature (center column), and precipitation (right column), determined by means of Cox proportional hazard modeling and model selection via AIC. Climate anomalies are the deviations of the variable from its long-term mean. A relative hazard of 1.2 indicates a 20% increase in mortality relative to a year with average climatic conditions. MAM = spring, JJA = summer, DJF = winter, previous = previous years' climate anomaly, current = current years' climate anomaly

Figure 3.

Relative mortality hazard in Europe's forests derived from remotely sensed net primary productivity (NPP). Isolines and colors show the variation in relative mortality hazard with remotely sensed mean NPP and the relative change in NPP in the previous two years. Results are derived from a Cox proportional hazard model, and predictions (envelope) are constrained to the range of the available observations (dots)

Table 1

Mean annual mortality rates in Europe's forests. The average share of trees that died per year between 2000 to 2012 is given by ecoregion and age class. N_p is the number of plots, N_t the total number of trees analyzed per stratum. Irregul. represents plots with an irregular age structure, containing uneven-aged forests. See Fig. S1 for the delineation of ecoregions

Mean mortality (% per year)		N_p (N_t)	Age class (years)							Irregul.	All
			0–20	21–40	41–60	61–80	81–100	101–120	>120		
Ecoregion	Northern Europe	8,706 (85,900)	0.53	0.15	0.37	0.50	0.53	0.34	0.39	0.58	0.40
	Central-western Europe	1,605 (49,065)	0.37	0.39	0.43	0.20	0.24	0.23	0.27	0.24	0.31
	Central-eastern Europe	1,509 (42,279)	0.38	0.44	0.35	0.35	0.33	0.27	0.12	0.00	0.34
	South-western Europe	1,032 (34,612)	3.18	1.35	0.98	0.70	0.66	0.17	0.25	1.05	1.39
	South-eastern Europe	778 (24,039)	0.14	1.39	1.51	1.01	0.56	3.11	0.48	0.31	1.20
All		13,630 (235,895)	0.82	0.46	0.50	0.49	0.46	0.40	0.37	0.69	0.50