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Increased Central European forest mortality explained by higher
harvest rates driven by enhanced productivityMarieke Scheel^{1,*} , Mats Lindeskog¹, Benjamin Smith^{1,2}, Susanne Suvanto^{3,4} and Thomas A M Pugh^{1,3,4}¹ Department of Physical Geography and Ecosystem Science, Lund University, 22362 Lund, Sweden² Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia³ School of Geography, Earth and Environmental Sciences, University of Birmingham, B15 2TT Birmingham, United Kingdom⁴ Birmingham Institute of Forest Research, University of Birmingham, B15 2TT Birmingham, United Kingdom

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E-mail: marieke.scheel@gmail.com**Keywords:** tree mortality, harvest, forest management, climate, CO₂ fertilisation, European forestSupplementary material for this article is available [online](#)

Abstract

Increasing tree growth and mortality rates in Europe are still poorly understood and have been attributed to a variety of drivers. This study explored the role of climate drivers, management and age structure in driving changes in tree mortality rates in six Central European countries from 1985 to 2010, using the process-based vegetation model LPJ-GUESS. Simulations show a strong positive trend in canopy mortality rates in Central Europe, consistent with satellite observations. This trend was explained by an assumed increase in managed thinning in response to a modelled increase in forest productivity caused by climate change and rising atmospheric CO₂ concentration. Simulated rates of canopy mortality were highly sensitive to the minimum tree size threshold applied for inclusion in the rate calculation, agreeing with satellite observations that are likely to only capture the loss of relatively large trees. The calculated trends in mortality rate also differed substantially depending on the metric used (i.e. carbon, stem or canopy mortality), highlighting the challenge of comparing tree mortality trends from different observation types. We conclude that changes in forest productivity and management in combination can profoundly affect regional-scale patterns of tree mortality. Our findings underscore the fact that increasing forest mortality can occur without reductions in forest growth when mediated by management responses to increasing productivity.

1. Introduction

In recent decades, forest growth rates have been observed to accelerate worldwide (e.g. Notaro *et al* 2005, Pretzsch *et al* 2014), with associated drivers including increasing atmospheric CO₂ concentrations (e.g. Friend *et al* 2014), increasing temperatures (Myneni *et al* 1997) and atmospheric nitrogen (N) depositions (Laubhann *et al* 2009). At the same time, tree mortality rates are increasing in many parts of the world (e.g. van Mantgem *et al* 2009, Senf *et al* 2018, Hubau *et al* 2020), a trend that has mainly been attributed to deleterious impacts of climate change, such as reduced precipitation (Archambeau *et al* 2020) or soil water availability (Birami *et al* 2018), but may also be linked to increased growth rates (Brienen *et al* 2020). In Europe, disturbances like windthrow,

forest fires and bark beetles have caused increasing damage in European forests (Senf and Seidl 2021) and are projected to increase further in the future (Seidl *et al* 2017). However, stand structure and management can also contribute to changing mortality rates. In Europe, forest demography has changed notably since the 1950s, with average forest stand age becoming lower (Vilén *et al* 2012), as a consequence both of shorter rotation times, and regrowth of forests on land formerly used for agriculture or other purposes (Hunter and Schuck 2002). Younger stands typically exhibit higher growth rates and lower losses of biomass through mortality than older stands. Since the 1950s, the ratio of harvest relative to the available woody biomass has been decreasing in Europe, as net primary production (NPP) increased faster than harvest rates (Ciais *et al* 2008).

In addition to changing mortality rates resulting from climate-related stress, more frequent disturbances or a more intensive harvest regime, increasing forest growth rate can affect tree mortality rate through intensified competition (Ruiz-Benito *et al* 2013, Luo and Chen 2015, Needham *et al* 2020). The self-thinning rule is a well-established principle of stand dynamics, whereby the evolution of stand biomass and stand density follows a log-linear relationship, along which young stands have a high density and low biomass and, as they mature, decrease in density due to the mortality of suppressed trees as total biomass increases (Yoda *et al* 1963, Westoby 1984). It follows that accelerated forest growth would be expected to lead a current forest stand of a certain age to consist of fewer trees that are larger in size than in a forest stand of the same age in the past (Pretzsch *et al* 2014). In other words, higher growth rates speed up self-thinning, reflected in higher mortality rates (Luo and Chen 2015, Lu *et al* 2019). As managed thinning activities seek to reduce pressure of competition between trees, the same acceleration of forest dynamics would be expected in a human-thinned forest. It is hence unclear how more favourable growing conditions (e.g. through CO₂ fertilisation or an extended growing season) versus worse growing conditions (e.g. water or other resource limitations) contribute to observed increases in tree mortality, compared to the other factors like historical perturbations of forest age structure and changes in harvest rates.

Senf *et al* (2018) used Landsat time series to show that the annual canopy mortality rate in Austria, Czechia, Germany, Poland, Slovakia, and Switzerland more than doubled between 1984 and 2016. Canopy mortality was detected based on changes in multiple spectral indices and defined as ‘percentage of forest area in which the dominant tree layer experienced a discrete mortality event’ (Senf *et al* 2018). It included the death of trees from any cause, including harvest. However, a clear attribution of the drivers of the observed canopy mortality increase in Senf *et al* (2018) is lacking. The increase in canopy mortality was suggested by Senf *et al* (2018) to be caused by the broad scale processes of changes in land use and especially increased harvest rates, particularly through thinning (as opposed to clear-cut) activities, due to changes in silvicultural practices. Generally, Senf *et al* (2018) concluded that stands with a high growing stock (GS) and/or large stand areas were affected more strongly by mortality, with fewer (but larger) trees dying in those stands than in the past. This was interpreted by Senf *et al* (2018) to suggest that decreasing carbon residence time and higher mortality might cancel out the general positive trend in forest growth. Spikes in European forest mortality in recent decades have been shown to be connected to droughts in Europe between 1986 and 2016 (Senf *et al* 2020), as well as to other climate extremes such as storms (Senf and Seidl 2021), but whether or not

climate change stress, i.e. changes in temperature and precipitation, contributes to the underlying trend is unclear.

This study aims to assess the extent to which increases in competition and changes in forest management might explain observed increases in canopy mortality in forests in six Central European countries (Austria, Czechia, Germany, Poland, Slovakia, and Switzerland) from 1985 to 2010. Using a process-based vegetation model to reconstruct forest productivity and stand dynamics based on first principles, we infer tree mortality rates relative to canopy area, biomass and stem number. First, the ability of the model to reproduce the observed canopy mortality rates is confirmed. Results from forcing the model with different putative drivers of mortality, i.e. changes in CO₂ concentration, climate and harvest, are then compared to disentangle the potential role of each driver in explaining observed mortality trends.

2. Methods

2.1. Vegetation model and simulation setup

We used the LPJ-GUESS model (v4.0, r11054) as described by Lindeskog *et al* (2021). LPJ-GUESS has been extensively evaluated against observations at both continental and country scale in Europe, including vegetation, soil, litter and ecosystem carbon stocks, net ecosystem carbon exchange, GS, net annual increase, harvested carbon, and natural mortality (Lindeskog *et al* 2021) as a function of climate, soil type and management assumptions.

LPJ-GUESS simulates forest growth and structure-function dynamics using multiple replicate 1000 m² patches, comprising age cohorts of co-occurring trees of multiple species or plant functional types (PFTs). Mortality and recruitment, applied stochastically, and individual growth governed by microenvironment (including effects of evolving stand structure on availability of light and soil resources), affect compositional, structural and demographic stand development. The model thus generates a distribution of stands of different ages, composition and vegetation structure approximating that in a real forest landscape. LPJ-GUESS explicitly differentiates mortality causes resulting from resource stress via carbon balance (including self-thinning), age, stand-replacing natural disturbance, wildfire and harvest.

The simulation setup followed Lindeskog *et al* (2021), except that mortality rates were output as a function of cause and stem diameter class and 100 replicate patches per grid cell were simulated to reduce stochastic noise in the outputs. This version of LPJ-GUESS does not include prognostic simulations of natural disturbances, so a mean return time of 400 years for generic, patch-destroying disturbances was applied as in Lindeskog *et al* (2021). Harvest as

Table 1. Settings of the six different simulations run in LPJ-GUESS, including the code they will be referred to in the rest of the paper.

Code	Description
S_{PNV}	Potential natural vegetation (PNV)
S_{nothin}	Forest age structure initialisation without thinning
S_{man}	Forest age structure initialisation with thinning (managed)
	Forest age structure initialisation with thinning, with the following settings
$S_{man,clim}$	All drivers but climate fixed to the repeated and detrended values of 1901–1930
S_{man,CO_2}	All drivers but CO_2 concentration fixed to the repeated and detrended values of 1901–1930
$S_{man,N}$	All drivers but Nitrogen deposition fixed to the repeated and detrended values of 1901–1930

thinning was simulated as automatic thinning, i.e. if a certain density threshold was reached trees above the threshold were removed, starting with the youngest, emulating standard silvicultural practice in the absence of detailed breakdowns of spatial variation in thinning practices. Major European tree species were simulated explicitly, with less common species represented by aggregate PFTs (table S1). The simulations were driven by historic monthly temperature, radiation and precipitation data from the CRU-NCEP dataset at a resolution of $0.5^\circ \times 0.5^\circ$ (Wei *et al* 2014), atmospheric CO_2 concentrations were sourced from the global carbon project (Le Quéré *et al* 2018) and nitrogen deposition rates from Lamarque *et al* (2011).

Age structure initialisation was performed following Lindeskog *et al* (2021). First the model was spun-up for 1200 years to establish the potential natural vegetation (PNV) species composition and carbon pools based on detrended 1901–1930 rates for climate, atmospheric CO_2 concentration from 1901 and nitrogen deposition data from 1850–1859. From 1860 onwards, the PNV stands were gradually replaced by managed forest stands in clearcut harvest events, to match the observed age composition and structure in the year 2010 (Poulter *et al* 2019). In total, 474 grid cells of $0.5^\circ \times 0.5^\circ$ were run, covering parts of Austria, Germany, Czechia, Poland, Slovakia and Switzerland classified as forest in 2010 in the EFI Tree species map (Brus *et al* 2012) and further masked by the forest age dataset (Poulter *et al* 2019). Biomass removed to initialise the age structure was assumed to be harvest. The harvested rate per country due to the initialisation of age structure was compared with satellite observations of clearcut harvested area (Ceccherini *et al* 2020) and total forest area (FAO 2021) (figure S1). For further validation, clearcut, thinning and natural mortality rates were tested against National Forest Inventory (NFI) data in Germany (figures S2 and S3). Model output for the years 1985–2010 was compared to canopy mortality observed by Senf *et al* (2018).

Six different simulations were run to allow the attribution of drivers to tree mortality (table 1).

2.2. Data processing

We defined canopy mortality as crown area loss ($m^2 \text{ yr}^{-1}$) divided by crown area (m^2), carbon

mortality as biomass loss ($kg [C] m^{-2} \text{ yr}^{-2}$) divided by total woody biomass ($kg [C] m^{-2}$) and stem mortality as stem loss divided by total stem number. Crown area, stem number and biomass were all explicitly simulated by LPJ-GUESS, with mortality rates calculated annually for each grid cell. Median rates of each year from all grid cells of a country and the whole region were then calculated. A threshold of 10 cm stem diameter at breast height (DBH) was applied for carbon and stem mortality. Canopy mortality only considered trees in the main canopy (supplementary methods) and was calculated using different DBH thresholds, excluding trees below the threshold. A threshold of 10 cm was applied to canopy loss and area for the general analysis, with larger thresholds used to explore the comparison to the mortality rates reported by Senf *et al* (2018).

Mortality rates were also calculated for each mortality mechanism within LPJ-GUESS, i.e. carbon balance, age, disturbance, fire, and harvest. Model output was analysed using MATLAB (The MathWorks Inc 2020), including the packages *polypredci* (Star Strider 2020) and *brewermap* (Stephen 2021).

3. Results

3.1. Comparing simulated canopy mortality to observed canopy mortality

Canopy mortality rates from S_{man} showed a trend similar to the canopy mortality trend observed by Senf *et al* (2018) in all countries, except Slovakia, when applying a threshold for trees with $DBH < 10 \text{ cm}$ (figures 1(a)–(f)). However, the simulated rates were around two to three times the canopy mortality values observed by Senf *et al* (2018) when using a DBH threshold of 10 cm in the canopy mortality calculation (table 2). In Slovakia, the slope in S_{man} was, contrary to the positive slope observed by Senf *et al* (2018), close to zero (table 2, figures 1(e) and S4).

Simulated mortality rates are much higher for small trees (figure 1(g)), and imposing a higher DBH threshold on trees contributing to the canopy mortality in S_{man} allowed us to find the most appropriate subset of trees to reproduce the mean canopy mortality observed by Senf *et al* (2018), with nonsignificant differences for Austria and Czechia

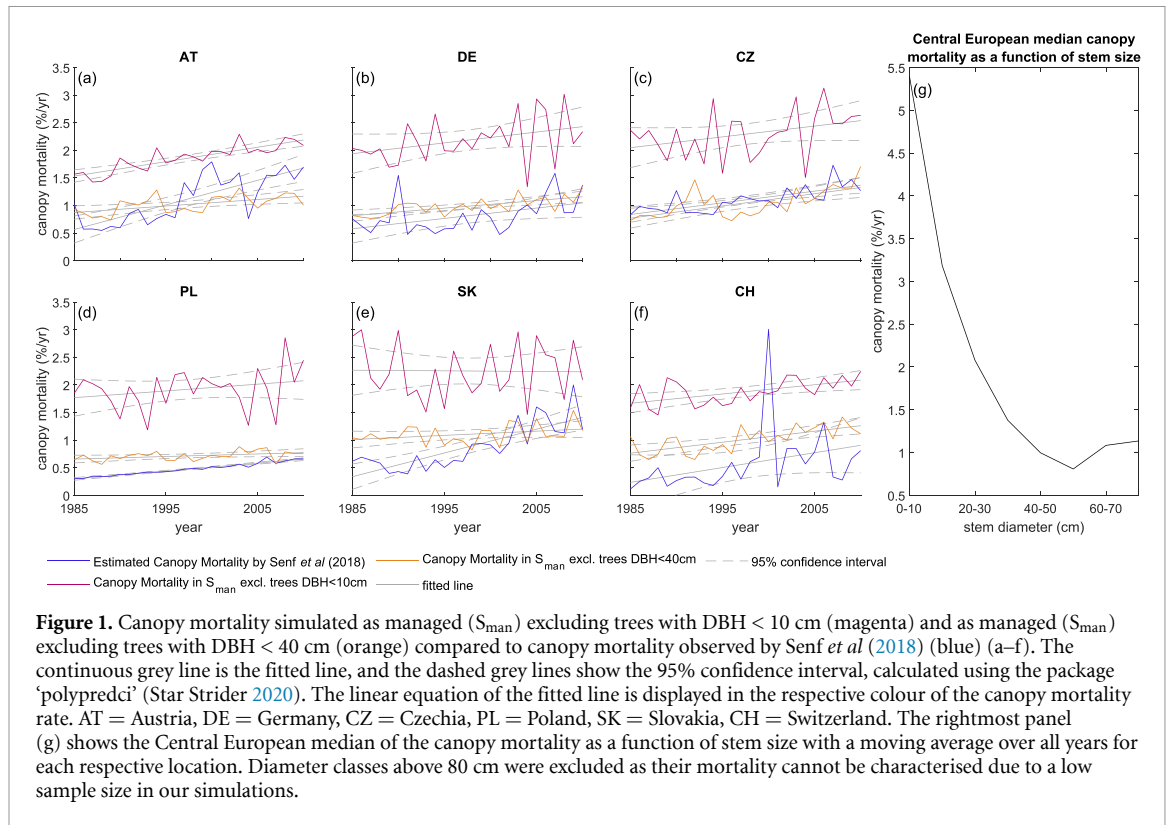


Table 2. Mean \pm standard deviation and slope \pm standard error (SE) of canopy mortality in the time series in S_{man} excl. trees with DBH < 10 cm and with DBH < 40 cm compared to those measures of data provided by Senf *et al* (2018). Value ranges that do not agree within 2SE with those from Senf *et al* (2018) are shown in light grey.

	S_{man} , DBH ≥ 10 cm		S_{man} , DBH ≥ 40 cm		Senf <i>et al</i> (2018)	
	Mean (%yr $^{-1}$) \pm SE	Slope (% points yr $^{-1}$) \pm SE	Mean (%yr $^{-1}$) \pm SE	Slope (% points yr $^{-1}$) \pm SE	Mean (%yr $^{-1}$) \pm SE	Slope (% points yr $^{-1}$) \pm SE
AT	1.86 \pm 0.05	0.026 \pm 0.003	1.02 \pm 0.03	0.012 \pm 0.003	1.12 \pm 0.08	0.045 \pm 0.007
DE	2.18 \pm 0.08	0.020 \pm 0.010	0.99 \pm 0.03	0.014 \pm 0.003	0.81 \pm 0.06	0.019 \pm 0.007
CZ	2.29 \pm 0.08	0.020 \pm 0.010	1.05 \pm 0.05	0.022 \pm 0.005	1.10 \pm 0.04	0.021 \pm 0.004
PL	1.92 \pm 0.07	0.012 \pm 0.010	0.71 \pm 0.02	0.005 \pm 0.002	0.47 \pm 0.02	0.014 \pm 0.001
SK	2.25 \pm 0.10	−0.001 \pm 0.013	1.10 \pm 0.03	0.008 \pm 0.004	0.87 \pm 0.08	0.043 \pm 0.007
CH	1.88 \pm 0.04	0.017 \pm 0.005	1.01 \pm 0.04	0.020 \pm 0.004	0.57 \pm 0.11	0.027 \pm 0.014

and comparable magnitudes for the other countries (table 2). An investigation of cut-off heights showed that trees DBH ≥ 40 cm yielded the closest agreement in terms of slope and mean (table S2). In Czechia, the estimates from the LPJ-GUESS model (DBH ≥ 40 cm) had a nonsignificant difference to that of Senf *et al* (2018) for both the mean and slope (table 2, figures 1(a), (c) and (f)). For Austria, Poland and Slovakia, the slope was significantly underestimated in S_{man} (DBH ≥ 40 cm, table 2).

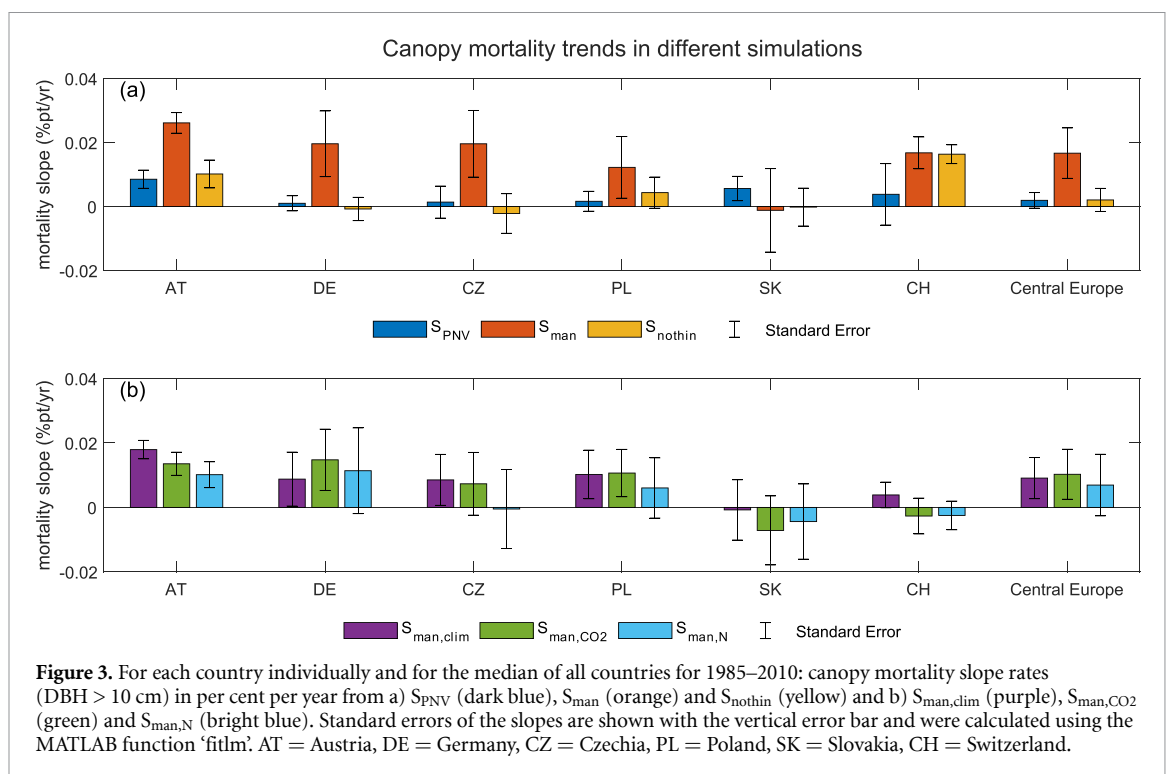
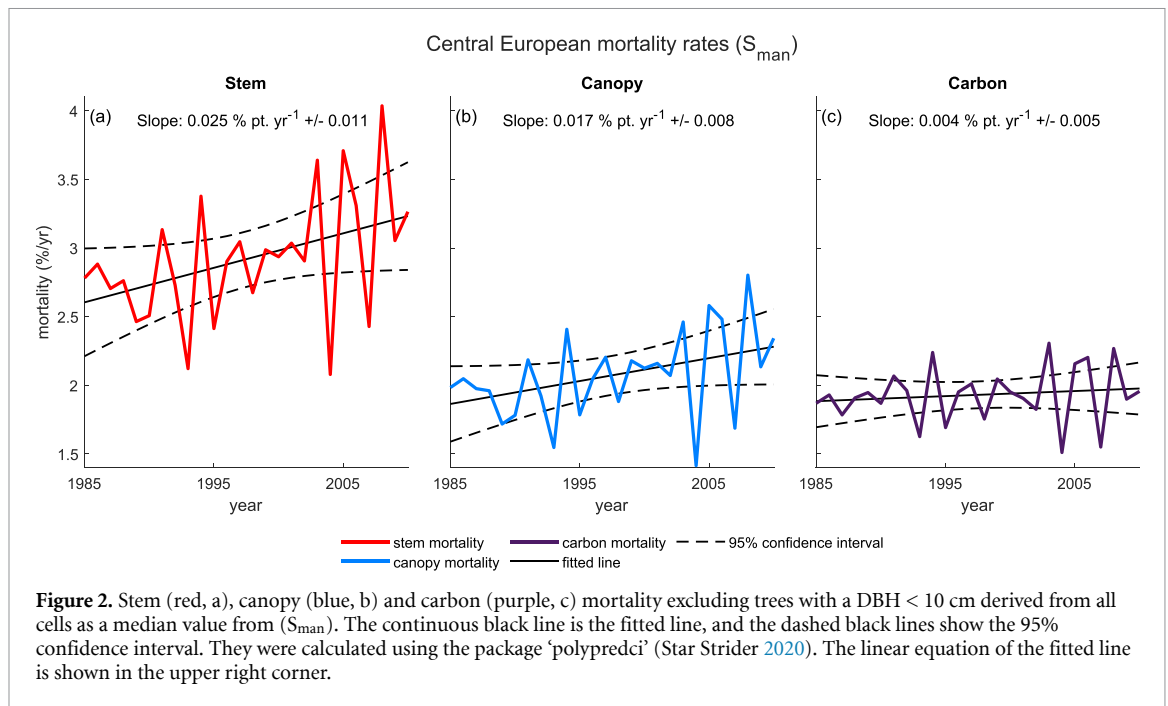
3.2. Influence of mortality metric

The median mortality rates (DBH ≥ 10 cm) across Central European forests showed different trends and orders of magnitude for the different measures of tree mortality (figure 2). Stem mortality showed the highest mean mortality rate

of $2.92 \pm 0.09\% \text{yr}^{-1}$ and the steepest increase in mortality rate (figure 2(a)). Canopy mortality had a lower mean with $2.07 \pm 0.06\% \text{yr}^{-1}$ and slope (figure 2(b)). The carbon loss rate showed the lowest order of magnitude with a mean of $1.93 \pm 0.04\% \text{yr}^{-1}$ and a slope close to zero (figure 2(c)). A linear regression using the MATLAB function ‘fitlm’ was conducted. $H_0: \beta = 0$ with $\alpha = 0.05$ could be rejected for stem ($p = 0.035$) and canopy mortality ($p = 0.045$), thus accepting $H_A: \beta \neq 0$. For carbon mortality H_0 could not be rejected ($p = 0.5$).

3.3. Drivers of mortality

Canopy mortality in S_{PNV} , which included only environmental effects and no harvest, showed significant but small positive slopes in Austria and Slovakia; and slopes indistinguishable from zero for the other

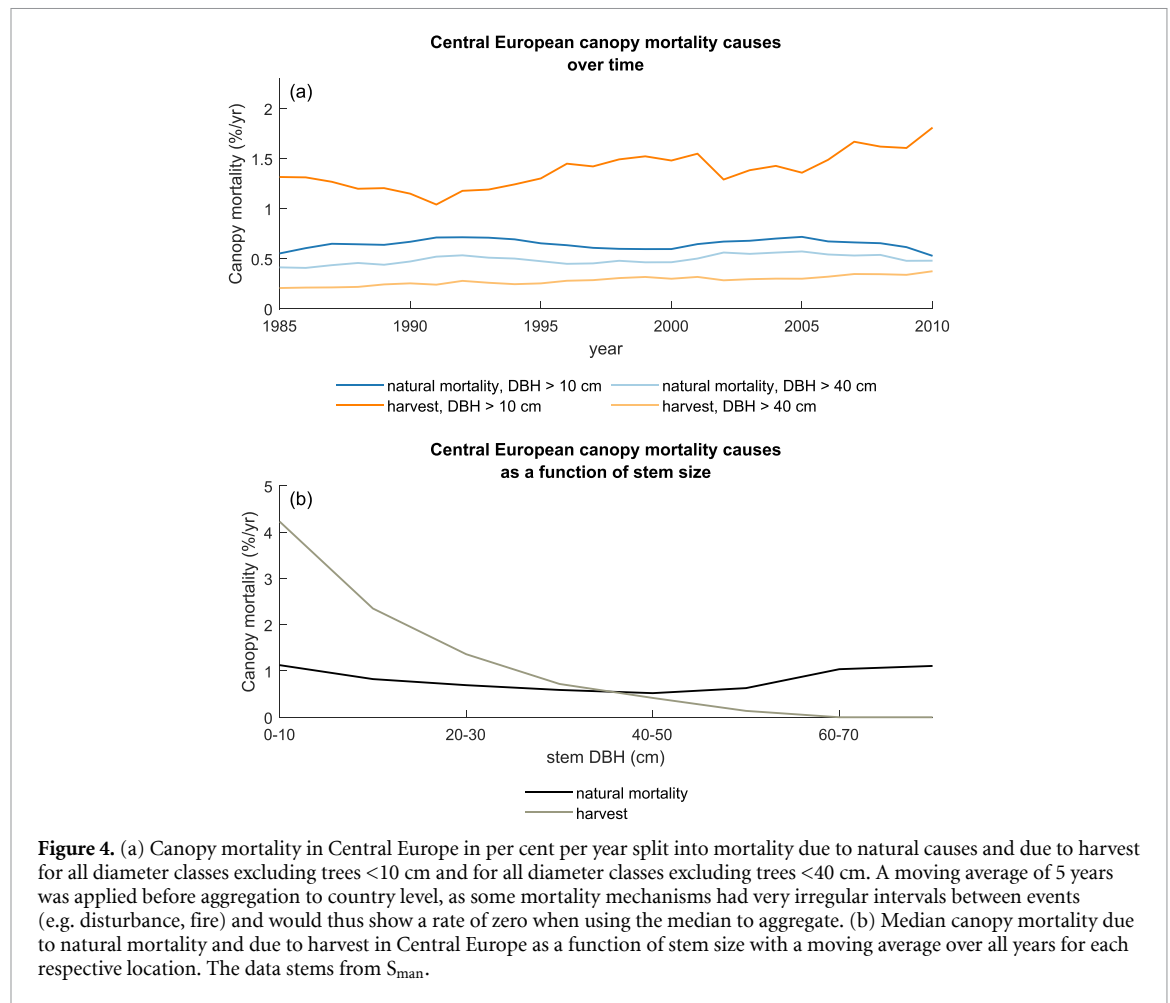


countries (figure 3(a)). In contrast, canopy mortality in S_{man} displayed a positive trend in nearly all countries. The canopy mortality in S_{nothin} showed a slope similar to that seen in S_{PNV} in all countries but Switzerland. In the latter, the slope was close to that in S_{man} . For all countries together, only the canopy mortality in S_{man} showed a positive trend.

In S_{PNV} , trees with a diameter of about 40–60 cm held most of the total stand biomass (except from Switzerland), a characteristic that strengthened over time (figure S4). In S_{man} , the total stand biomass

was distributed relatively evenly over all size classes (figure S5).

Both climate and CO_2 concentration were significant drivers of the positive trend in tree mortality rate in Central Europe (figure 3(b)). Nitrogen deposition did not cause a significant mortality trend in any country but Austria. In individual countries the contributions of climate and CO_2 were often non-significant, despite significant trends when all drivers were included, reflecting important contributions of multiple drivers.



3.4. Mortality mechanisms

The canopy mortality caused by harvest ($\text{DBH} \geq 10$ cm) showed the highest rate, as well as the steepest increase, 1985–2010 in Central Europe compared to the natural mortality (figures 4 and S6). When only including trees with $\text{DBH} \geq 40$ cm, the canopy loss rate driven by harvest is lower than that driven by natural causes. The natural canopy mortality did not show any trend for canopy mortality. Canopy mortality in S_{PNV} likewise showed no trend (figure S7). The high mortality rate for smaller tree sizes was mainly driven by harvest, which caused relatively little mortality for larger tree sizes. Natural canopy mortality was relatively similar for all tree sizes.

4. Discussion

4.1. Comparison with observed canopy mortality

The canopy mortality in S_{man} reproduced the canopy mortality observed by Senf *et al* (2018) fairly well, when only trees with $\text{DBH} \geq 40$ cm were considered. Since the observed canopy mortality was based on Landsat satellite data, the canopy mortality observations could have only captured the mortality of larger trees in the overstory. Losses of smaller trees are unlikely to be detected due to masking

by the upper canopy and the comparatively coarse resolution (30 m) of the Landsat data. The mortality rate from LPJ-GUESS, on the other hand, takes all trees above the DBH threshold into account. The threshold of 40 cm was solely based on the fit of the simulated canopy mortality rate to that observed by Senf *et al* (2018). This mortality rate likely excludes a substantial part of the overstory in many stands, as the mean overstory diameter in European forests was found to be approximately 14–32 cm (Pach and Podlaski 2015). We cannot distinguish between the possibilities that LPJ-GUESS is overestimating the canopy mortality rate of the overstory, or that the Landsat mortality product is insensitive to mortality of trees less than ca. 40 cm DBH. However, it is well established that mortality rates are typically higher for small trees (Neumann *et al* 2017), as simulated in LPJ-GUESS (figure 1), it is therefore unlikely that small tree death would produce an appreciable spectral signal at the scale of a Landsat pixel, it is likely that true canopy mortality rates are higher than estimated by Senf *et al* (2018). In Slovakia, the modelled canopy mortality trend did not show a significant positive trend. Tree mortality in Slovakia in the 2000s was primarily driven by storm and bark beetles (Nikolov *et al* 2014), which has likely driven the positive trend in canopy mortality shown by Senf *et al*

(2018) and which could not be captured in our setup.

4.2. Different mortality measures

Measures of tree mortality are often considered to be interchangeable, and it is therefore common to use a single measure of mortality (Barlow *et al* 2003, Byer and Jin 2017). Large-scale events that particularly affect larger trees are often underestimated in stem mortality (Chambers *et al* 2013), while changes in the understory may not be resolved in carbon and canopy mortality. Stem mortality is a more sensitive metric of mortality of younger trees, as the number of saplings and small stems in a given area is typically much higher than the number of adult tree stems (Westoby 1984). The increase in growth rates together with harvest as thinning likely shifted the overall mortality rate more towards smaller trees, reflected in higher stem mortality rates (figure 2). The nonsignificant trend of the carbon mortality rate (figure 2) could be explained by a positive trend in forest biomass in all countries, the slope of which exceeds the increase in mortality rate (figure S8). The canopy mortality rate is not so strongly affected as canopy area is already maximised across much of the region. The strongly positive trend in biomass is consistent with results reported from forest inventories (Ciais *et al* 2008). Our results show that it is important to consider mortality trends in the context of the particular mortality metric being applied and to ideally include calculations of more than one metric when assessing changes in tree mortality.

4.3. Mortality trends

The positive canopy mortality trend in S_{man} was largely driven by thinning (figure 3), shown by S_{nothin} , where the canopy mortality slope was close to zero. This result is consistent with the interpretation of Senf *et al* (2018), who suggested the increase in mortality rates to be caused by forests recovering from past land use and increased harvest in the form of thinning. Thinning is triggered in LPJ-GUESS when the stand reaches a certain stand density (Lindeskog *et al* 2021), clearly linking the increase in thinning to an increase in NPP. Despite higher productivity, stand densification is inhibited since managed thinning is triggered by a density threshold (figure S5).

NPP increased only slightly over time for all countries (figure S9). NPP can be used as an indicator for mortality caused by increased competition (Stephenson *et al* 2011). However, thinning also reduces whole stand NPP. The NPP trend in S_{PNV} showed a slightly positive trend, albeit with a high standard error. Interestingly, the self-thinning rate in S_{PNV} did not show a trend, although it is also driven by an increase in NPP. This can likely be attributed to a shift in biomass distribution towards older trees (figure S4). Self-thinning in LPJ-GUESS is partly a function of crown area, and as crowns

of larger trees no longer expand (maximum simulated crown area is capped at 50 m², Smith *et al* 2014) this tends to exclude larger trees from self-thinning. Following the allometric function of tree growth applied in LPJ-GUESS (Smith *et al* 2014), trees with DBH > 37 cm (shade-intolerant) and DBH > 50 cm (shade-tolerant) will have reached the maximum crown area.

Both changes in climate and atmospheric CO₂ concentration added to the increase in canopy mortality via improved growth conditions that led to faster thinning (figure 3(b)). CO₂ fertilisation has been shown to increase NPP by enhancing photosynthesis rates (Leakey *et al* 2009), while higher temperatures can (up to a certain threshold) increase NPP by lengthening the growing season (Harsch *et al* 2009). The drivers can amplify each other as trees can benefit from CO₂ fertilisation longer because of warming-induced growing season extension (Bellassen *et al* 2011).

Biomass removed to initialise the observed stand age structure in 2010 is assumed to be harvest in the LPJ-GUESS model (Lindeskog *et al* 2021), but might also come about due to natural disturbances. The two largest abiotic causes of natural disturbances, wildfires and storms, are estimated to be responsible for an annual disturbance of ca. 270 000 ha (1986–2016), thus an annual rate of ca. 0.1% of the total forested area in Europe (227 million ha in 2020) (Senf and Seidl 2021). Because the wood from disturbed trees is often salvaged, leading to reductions in harvest the following years, the distinction between planned harvest and disturbance for mortality trends may in any case be blurred.

4.4. Mortality loss causes

Managed thinning most strongly affected smaller trees (figure 4), as shown by the large difference between the canopy loss rates driven by harvest excluding trees with DBH < 10 cm and with DBH < 40 cm. The simulated biomass harvest thinning rates were slightly underestimated compared to NFI data from Germany (figure S2(b)), likely since NFI data will include salvage logging that LPJ-GUESS cannot capture. This is supported by the good fit of overall biomass mortality rates (natural and harvest) of NFI and LPJ-GUESS (figure S3); natural mortality rates estimated from NFI will tend to be lower than in reality due to salvage logging included in the harvest rate.

Natural mortality, however, affected all diameter sizes relatively evenly and did not show any trend. Additionally, the natural mortality rates were very similar for all size classes ≥ 10 cm and for all size classes ≥ 40 cm. This aligns with the finding of the higher rate for smaller trees being mainly driven by managed thinning. However, it should be recognised that the model as applied here does not include all

climate-related mechanisms that might conceivably be implicated in observed mortality trends. In particular, tree loss due to wind and insect (e.g. bark beetle) damage is not included. Drought effects leading to carbon starvation are included, but hydraulic failure due to xylem embolism is not built into this version of the model (Pugh *et al* 2020). Nonetheless, even in the absence of any simulated increase in mortality due to drought stress, managed thinning was able to produce similar canopy mortality rates to those in the observations. There is evidence, however, that hydraulic failure has become more important since 2010 (Schuldt *et al* 2020). The thinning itself is driven by growth, which is a key driving process in the LPJ-GUESS model (Smith *et al* 2014, Pugh *et al* 2020) as in natural ecosystems. Previous analysis of changes in natural disturbance rates is insufficient to explain observed forest mortality patterns for our study area (Senf *et al* 2018, Senf and Seidl 2021). Thus, the omission of some climate-related mechanisms of tree death in our model is not expected to change the conclusions of this study.

5. Conclusion

The strong positive trend in canopy mortality observed in Central Europe over recent decades can be largely explained by increased harvest in the form of thinning. The increase in biomass removal via thinning follows from an increase in forest productivity (NPP), which is driven by both changes in climate and CO₂ fertilisation. Although changing natural disturbances are not needed to explain the trend in canopy mortality rates from 1985 to 2010, they can explain inter-annual variability and maxima in canopy mortality (Senf and Seidl 2021).

Trends are sensitive to the mortality metric used. Failure to take account of the different information contained in metrics of stem, canopy and biomass mortality may lead to misinterpretations of whether and in what ways forest dynamics are changing. Ideally, a multi-metric approach should be employed to properly characterise trends in tree mortality. Additionally, mortality rates are highly sensitive to the threshold used to exclude small trees.

Whilst our results identify a combination of increased forest productivity driven by environmental change and responsive forest management as the primary causes of observed increases in canopy mortality in the period 1985–2010, a continuation of these trends over the coming decades is far from certain. Extreme heatwaves in 2018 and 2019 have imposed severe stress on Central European forests, reducing productivity and causing increased tree mortality (Schuldt *et al* 2020). These events have led to unprecedented outbreaks of bark beetles in some regions (Schuldt *et al* 2020) as well as drought-induced tree mortality. If such events become more frequent, as anticipated over the remainder of this

century (Allen *et al* 2015), then they may override the effect of productivity increase and dominate future trends in tree mortality.

Data availability statement

The data that support the findings of this study are openly available at the following DOI: [10.5281/zenodo.6393790](https://doi.org/10.5281/zenodo.6393790). All code used for data analysis and figure generation is available at the following DOI: [10.5281/zenodo.7121257](https://doi.org/10.5281/zenodo.7121257).

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