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Perspectives for forest modeling to improve the representation of drought-related tree mortality

Perspektiven der Waldmodellierung zur verbesserten Darstellung der trockenheitsbedingten Baumsterblichkeit

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Abstract

We are currently observing increased tree mortality following multi-year drought events, particularly in low mountain ranges like the Harz Mountains in Germany, where over 70% of spruce stands have died. Forest models are useful tools for understanding the long-term effects of climate change on forest ecosystems, yet struggle to reproduce this massive dieback. In this study, we simulated spruce mortality in the Harz Mountains using five forest models (ForClim, FORMIND, 3-PG-Hydro, LPJ-GUESS, GOTILWA+) of very different complexity. Estimated from the crown condition survey, spruce mortality in the Harz region increased to values above 30% during recent drought years (2018–2020). We found that most models failed to capture these observed high mortality rates, although they showed a clear signal in reduced forest productivity during drought.

This discrepancy between the observed high spruce mortality and simulated forest dynamics highlights the need for improved modelling approaches to accurately represent tree mortality processes during and after extreme drought events. We discuss several perspectives for enhancing dynamic forest models by integrating missing processes prospectively. This includes novel (i) process-based drought mortality approaches, (ii) enhanced description of eco-physiological processes like plant hydraulics, (iii) data-driven and AI approaches, and (iv) improved representation of biotic damaging agents (i.e., insects and pathogens). Incorporating these perspectives into forest models has the potential to improve their ability to simulate forest dynamics under extreme drought, ultimately con-

tributing to the assessment of forest resilience and informing adaptive management strategies in Germany and beyond.

Keywords

forest models, simulation, spruce, Harz mountains, bark beetle

Zusammenfassung

Derzeit beobachten wir ein erhöhtes Baumsterben nach mehrjährigen Dürreperioden, insbesondere in Mittelgebirgen wie dem Harz in Deutschland, wo über 70 % der Fichtenbestände abgestorben sind. Waldmodelle sind nützliche Instrumente, um die langfristigen Auswirkungen des Klimawandels auf Waldökosysteme zu verstehen, können aber dieses massive Absterben nur schwer wiedergeben. In dieser Studie haben wir das Fichtensterben im Harz mit fünf Waldmodellen (ForClim, FORMIND, 3-PG-Hydro, LPJ-GUESS, GOTILWA+) von sehr unterschiedlicher Komplexität simuliert. Die anhand der Waldzustandserhebung geschätzte Fichtensterblichkeit stieg in den zurückliegenden Dürre Jahren (2018–2020) auf Werte von über 30 % pro Jahr. Wir stellten fest, dass die meisten Modelle diese beobachteten hohen Sterblichkeitsraten nicht simulieren konnten, obwohl sie ein deutliches Signal für eine verringerte Waldproduktivität während der Trockenheit in den Simulationsergebnissen aufwiesen.

Diese Diskrepanz zwischen der beobachteten hohen Fichtensterblichkeit und der simulierten Walddynamik unterstreicht die Notwendigkeit verbesserter Modellierungsansätze, um



die Prozesse der Baumsterblichkeit während und nach extremen Dürreereignissen besser darzustellen. In dieser Studie zeigen wir mehrere Perspektiven zur Verbesserung von Waldmodellen durch die Integration fehlender Prozesse auf. Dazu gehören (i) verbesserte prozessbasierte Ansätze zur Baumsterblichkeit nach Dürren, (ii) eine verbesserte Beschreibung ökophysiologischer Prozesse wie der Pflanzenhydraulik, (iii) datengetriebene Mortalitätsansätze und KI, (iv) eine verbesserte Abbildung biotischer Schadfaktoren (d. h. Insekten und Krankheitserreger) in Modellen. Die Einbeziehung dieser Perspektiven in Waldmodelle hat das Potenzial, deren Fähigkeit zur Simulation der Walddynamik bei extremer Trockenheit zu verbessern und letztlich zur Bewertung der Widerstandsfähigkeit von Wäldern und zur Information über adaptive Managementstrategien in Deutschland und darüber hinaus beizutragen.

Stichwörter

Waldmodelle, Simulation, Fichte, Harz, Borkenkäfer

Introduction

Forests play a key role in mitigating climate change by sequestering carbon, offer a high degree of biodiversity and are crucial for tourism and the timber industry (Anderegg et al., 2020). However, climate change poses a huge challenge for forests (Bonan, 2008; Hartmann et al., 2022). Besides the general rise in temperature, the increased occurrence of climatic extreme events such as storms, droughts and heatwaves is a further factor (Seidl et al., 2017; Brodribb et al., 2020; Patacca et al., 2023). These climatic extremes make forest landscapes drought-stressed and therefore susceptible to diseases. This has negative consequences for forests across Europe, where pests and diseases are spreading more frequently (Senf & Seidl, 2018; Warlo et al., 2025; Hartmann et al., 2025). Bark beetles, particularly in spruce forests, have become a major problem, causing widespread tree mortality, especially in areas under drought stress (Hartmann et al., 2025).

The forests in Germany have been severely affected by the prolonged droughts and heat waves of recent years (Senf et al., 2020; Senf & Seidl, 2021; Thonfeld et al., 2022; Holtmann et al., 2024). The latest results of the National Forest Inventory show that German forests are under severe stress, primarily due to climate change, drought and storms ('Bundeswaldinventur' BWI 2022; BMEL, 2024a). The weakened trees are also susceptible to infestation by pests such as bark beetles and fungi. Therefore, the majority of trees across Germany show signs of reduced vitality (~80%), especially common species such as spruce, pine, beech and oak (according to the national forest condition survey of Germany, 'Waldzustandserhebung' WZE; BMEL, 2024b).

Although the whole of Germany is affected by this problem, the low mountain regions are experiencing the highest forest losses nationwide due to climate change-related extreme events in the country (MWL, 2021). One highly discussed area under stress is the Harz mountain ecoregion in northern Germany, a relatively small mountain range, but quite distinctive with its rugged terrain and rich natural habitats. It

covers roughly 2,226 square kilometers. Compared to other low mountain ranges in Germany, the spruce-dominated Harz has suffered from a particularly large area of tree cover loss.

Climatic extreme events make spruce-dominated forests more susceptible to pests such as the bark beetle outbreaks (Seidl et al., 2014). According to latest estimates, around 71% of the spruce trees in the Harz have died since 2017 (Knapp et al., 2024), with many negative consequences for ecosystem services (e.g. loss of habitats), the release of carbon, but also the alteration of water and nutrient cycles. Large-scale tree mortality poses a major challenge to forest owners and forest administrations in Germany, as the quantities of damaged timber are enormous and there is often a lack of resources for rapid reforestation. The high mortality rate of spruce in the Harz Mountains during and after the drought 2018–2020 is thought to be the result of a complex interplay of factors, including bark beetle infestation, storms, forest fires, and hydraulic failure (NW-FVA, 2023).

Traditional approaches to forest management are reaching their limits due to the combined pressures of climate change, pest infestations, biodiversity loss, economic challenges, and the complexity of balancing ecological and economic objectives. The traditional approaches that sustained Germany's forests for centuries are no longer sufficient to cope with the scale and speed of environmental changes (Seidl et al., 2008; Bottero et al., 2021; Wessely et al., 2024). It is unclear what a resilient forest of the future under transient environmental conditions will look like, as the experience by foresters of recent decades is no longer sufficient. It is therefore important to assess future developments of forest ecosystems in a changing world in order to adapt the management of ecosystems to climate change. Observations and experiments alone are not enough to assess future forest development, as they can only cover a limited number of stressors as well as have a comparatively narrow timeframe in relation to upcoming decades under climate change. The use of dynamic models is therefore essential to better assess future forest development under the influence of climatic extremes (e.g., drought, heat), insect infestation, diseases, and forest fires (Schumacher & Bugmann, 2006; Shugart et al., 2018; Rammer et al., 2024).

Dynamic forest models play a key role in this regard. In recent decades, a large number of forest simulation models have been developed to simulate the dynamics of forest structure and species composition on annual, decadal and centennial time scales and to project the impacts of climate change and management interventions on future forest developments (Shugart, 1984; Bugmann, 2001; Maréchaux et al., 2021; Lindeskog et al., 2021; Bugmann & Seidl, 2022).

The ability of forest models to produce realistic simulations depends on both the incorporation of accurate ecosystem process knowledge and a robust data basis for parameterization, initialization, and testing (Huber et al., 2020). While there is plenty of data on tree growth and forest state (e.g., national forest inventories, monitoring programs, tree-ring measurements, experiments, remote sensing, etc.), data on tree mortality processes remain limited. This data scarcity contributes to the high uncertainty associated with modeling tree mortality processes, particularly in assessing the long-term response of forests to climate change (Bugmann et al.,

2019). The intention of forest model development should therefore be to improve the representation of tree mortality processes in forest models. It is important to ensure that not only the long-term average of tree mortality can be well mapped, but also the short- to medium-term response of trees to extreme climate events. However, increased model complexity does not necessarily lead to more accurate simulation results (Railsback & Grimm, 2019; Bugmann & Seidl, 2022). Moreover, there is no consensus on the level of complexity that is needed for accurately predicting drought-induced mortality (Meir et al., 2015). Some studies suggest that integrating findings from existing work (Desoto, 2021), via optimization algorithms (Wunder et al., 2006), statistical approaches (Petit-Cailleux et al., 2021), or probabilistic modeling (Hartmann et al., 2007; Vanoni et al., 2019), could enhance predictions without increasing complexity (Meir et al., 2015). Others, like McDowell et al. (2011), advocate for more mechanistic modeling approaches, such as integrating carbon starvation and hydraulic failure mechanisms.

Hydraulic failure and carbon starvation represent general drought-induced tree mortality mechanisms (Hajek et al., 2022). Hydraulic failure occurs when excessive transpiration and reduced soil water availability cause embolisms in the xylem, disrupting water transport (Vilagrosa et al., 2012). Carbon starvation results from a depletion of mobile carbohydrate pools due to ongoing stomatal closure. Stomatal closure prevents water loss (and thus hydraulic failure), but at the expense of photosynthetic assimilation which is essential to refill mobile carbohydrate pools that feed important life processes such as growth, repair and maintenance. Both mechanisms reduce productivity, increase vulnerability to biotic stressors (e.g. by weakening defense mechanisms), and can subsequently lead to tree mortality (Hajek et al., 2022). However, their interaction and their species-specific effects are still not fully understood (Allen et al., 2015; Obladen et al., 2021). Trugman et al. (2021) emphasize the importance of incorporating plant-level physiological factors and traits, site-specific conditions, and community-level interactions. There are indeed models that take into account carbon starvation (with varying degrees of complexity, such as the ED model, 3D-CMCC-FEM, etc.; Collalti et al., 2014; Ma et al., 2022) or hydraulic failure (e.g. MEDFATE model, De Cáceres et al., 2022). Some forest models instead use aggregated growth reduction factors or other stresses associated with a probability of tree mortality (e.g. 4C, Reyer et al., 2014).

Different approaches have been selected to model tree mortality in forest models, as they were developed for different research questions. In all forest models, approaches have been developed to simulate tree growth depending on environmental conditions (e.g., shading, soil water, etc.). For example, if future climate conditions become drier and hotter, the forest models will simulate changes in forest structure and dynamics. Whether these established approaches on climate-dependent tree growth and tree mortality will be sufficient to reproduce this massive tree mortality in the Harz Mountains (or in other regions of Germany and Europe) remains uncertain.

In this simulation study, we used different forest models to simulate spruce forest dynamics in the Harz Mountains from 2000 to 2023 and compared them with data showing mas-

sive regional tree mortality following a multi-year drought event. All the models used have integrated processes, so that the simulated forest dynamics are dependent on climatic conditions – but they differ in the level of detail of the modelled processes. The main question of this study is therefore: **Would forest models have been able to predict the massive spruce dieback in the Harz Mountains that has been observed after 2018?** The models have a different levels of detail, but tree mortality is always modelled, either constant, dependent on stand structure or dependent on climatic conditions. Whether one or more of these approaches are sufficient to reproduce the observed spruce dieback in the Harz Mountains remains unclear and will be tested here.

For this purpose, we applied the different forest models, that are based on widely different paradigms, different mortality approaches and drought response, to the same region in the Harz Mountains. After comparing the simulations of different models with the overserved spruce mortality rates, we discuss model development perspectives that could help us improve the prediction of future forest dynamics after climatic extreme events. Although we have examined a specific spruce-dominated forest area in Germany in this study, the model perspectives we propose are generally valid and independent of the tree species and should support future model development.

Simulation of multi-year drought events with models

The aim of this study was to simulate a representative spruce-dominated forest stand in the region of the Harz Mountains under the climatic conditions of the years 2000 to 2023, including the multi-year drought 2018–2020. We selected a total of five well-established models with which it was possible to simulate a representative spruce stand in the Harz Mountains and whose approaches for modeling tree mortality are partially different: 3-PG-Hydro, ForClim v.4.0.1 and v.4.1, LPJ-GUESS, GOTILWA+, and FORMIND (model descriptions see supplementary information S1). Please note that the standard parameterizations were used for all models, i.e. they were not adapted to the conditions in the Harz Mountains. All models were initialized on the basis of the same forest inventory data and used the identical climate data for simulation (see supplementary information S2 and S3). A 10 ha pure spruce stand with an initial basal area of approx. 45 m²/ha was simulated. Stand dynamics were simulated and tree mortality was analyzed for the period 2000–2023 for all models and compared with the average estimated spruce mortality based on the annual national crown condition survey (supplementary information S4).

Simulated tree mortality in non-drought years

In general, most of our model simulations show long-term mortality rates comparable to observed spruce mortality in the years 2000 to 2016, where no multi-year droughts occurred (Fig. 1A). Observed mortality averages 0.6% during this period, while the models predict mortality ranging from 0% to 1.4% (FORMIND: 1.4%, 3-PG-Hydro: 0.02%, ForClim v.4.0.1:

0.5%, ForClim v4.1: 0.6%, GOTILWA+: 0.0%, LPJ-GUESS: 0.2%; see Fig. 1A). However, we also found that the models are not able to capture the inter-annual variability of mortality rates. This is also because storm events in Germany (e.g. Kyrill in 2007) and the subsequent spread of pests in the damaged wood were not included in the modelling study. Furthermore, the importance of soil hydrology for the simulations and the impact of different sources of climate forcing data was not analyzed in this study (it is only briefly discussed in the supplementary information S1: ForClim).

The GOTILWA + and 3-PG-Hydro models show almost no mortality in the period 2000–2016, when no multi-year droughts occurred (Fig. 1A). LPJ-GUESS estimated an almost constant mortality rate in the range of observation (Fig. 1A). FORMIND generated an inter-annual variability with partly increased mortality in dry years. These mortality peaks were shifted by 1–2 years relative to the observed peaks. However, FORMIND's average simulated mortality rate was slightly higher than the observed rate. The two ForClim variants are qualitatively very similar and have similar synchronization issues as FORMIND. On average, ForClim matched the observed mortality in the non-drought period well but could not reach the large peaks in the dry years (e.g. mortality of 1.9% was observed in 2007 and ForClim simulates mortality of 0.4%;

Fig. 1A). The fact that most models were in good agreement with the mean observed tree mortality in periods without multi-year droughts is probably due to the fact that annual tree mortality did not vary much over long periods of time (in the range 0.5%–1%). Therefore, the long-term means of mortality, which can be derived from the National Forest Inventory or the crown condition survey, are a good approximation for tree mortality parameters. Briefly, in years without severe drought events or other disturbance events (e.g. storms), simpler modeling approaches are probably sufficient.

Simulated tree mortality during drought period 2018–2020

For the drought years, especially from 2018 onwards, large deviations between the model simulations and the spruce mortality estimated from the crown condition survey were observed (Fig. 1B). Annual observed spruce mortality increased to values above 30%, with an average of 23% for the years during the drought and after the drought (2018–2023). In contrast, most models showed almost no change in mortality compared to previous years (average values 2018–2023: FORMIND: 1.6%, 3-PG-Hydro: 0.02%, ForClim v4.0.1: 0.6%, ForClim v4.1: 19%, GOTILWA+: 4.5%, LPJ-GUESS: 0.3%; see Fig. 1B).

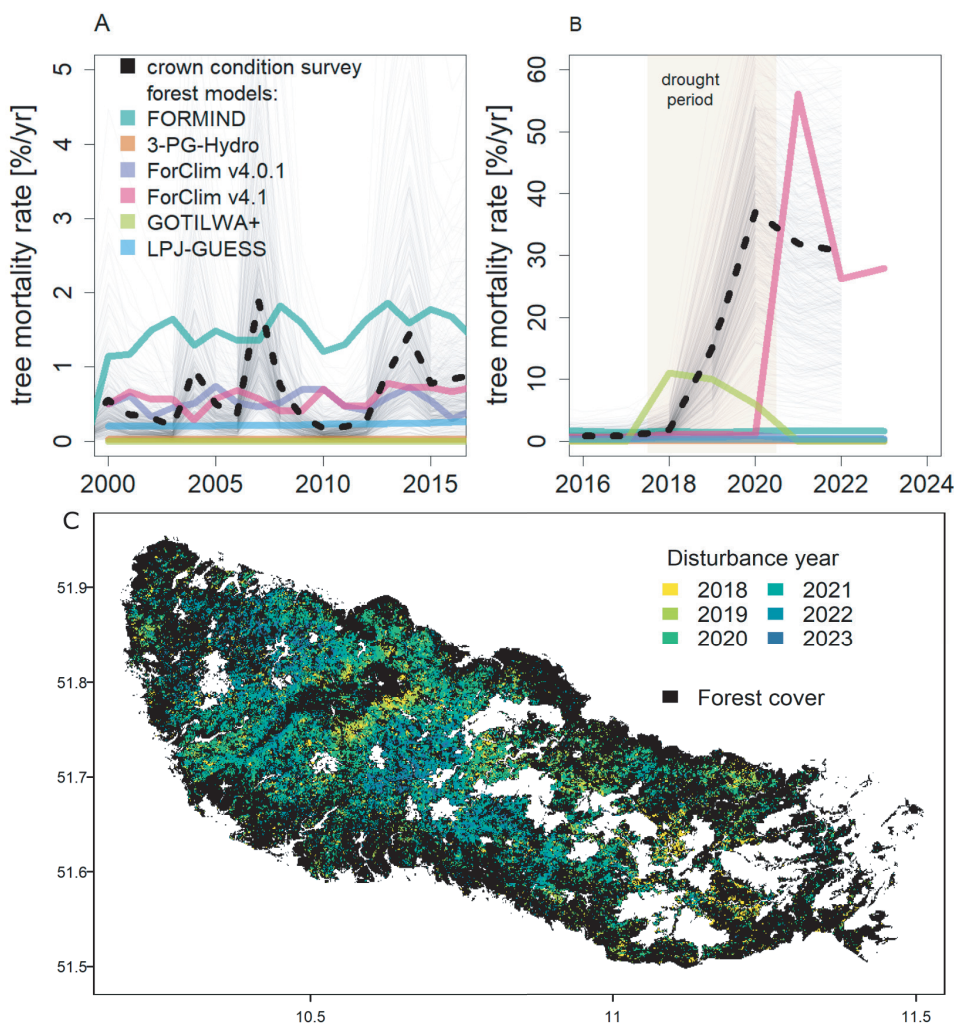


Fig. 1: Spruce mortality in the Harz Mountains from 2000 to 2023. The simulated spruce mortality of five forest models (colored solid lines) is compared with the estimated spruce mortality based on the annual national crown condition survey (black dashed line). A) Simulated tree mortality for the period 2000–2016. B) Simulated tree mortality during and after several years of drought. Please note the different scaling of the y-axis for A) and B). The orange zone indicates the years 2018–2020 with extreme drought conditions. The black dashed line is the mean mortality estimated from the crown condition survey across all spruce-dominated forest stands in the Harz Mountains, and thus serves as a reference for spruce mortality. The fine grey lines show the spruce mortality at 100 random locations in the region to demonstrate the spatial variability. C) Map of forest areas affected by disturbances from 2018 to 2023 in the Harz region (Viana-Soto & Senf, 2024).

The GOTILWA + model, which integrates a process-based approach to capture tree mortality, responded to the drought signal, resulting in an increase in spruce mortality in 2018 (11%) and 2019 (10%). While the onset of simulated drought-induced mortality was earlier than observations (1.8% in 2018), it captured well the magnitude in 2019 (15% of observed mortality). After 2020, however, mortality was 0% in the model compared to, for example, more than 30% in 2021 in the observations. This reflects the presence of non-linear effects and thresholds in the mortality formulations, but also the lack of a pest-induced mortality approach. It should be noted that GOTILWA + was not calibrated to the specifics of the studied region, using the setting of silver fir (*Abies alba* MILL.) from the Black Forest. However, it was partially able to capture the increase in tree mortality under multi-year drought conditions. This is a first indication that a process-based mortality approach can help to better represent such extensive tree mortality events.

The ForClim v4.1 model showed a sharp increase in tree mortality in the years 2021 to 2023, namely 56% in 2021, 26% in 2022, and 28% in 2023), with some of the simulated mortality rates significantly higher than the highest observations. The model delayed the onset of significant mortality events, with the highest mortality occurring in 2021, whereas field observations indicated substantial mortality already in 2020. Regardless of this shift, the mean simulated mortality during the drought period was 37% (2021–2023) and thus fits with the observed mortality 28% (2019–2022) in terms of magnitude. Please note that this model, and the other models in this study, do not include contributing factors (e.g. biotic stressors) such as bark beetle infestations, which are in this case known to have exacerbated tree mortality.

Unlike its predecessor (version 4.0.1), ForClim 4.1 explicitly distinguishes between predisposing and inciting factors that contribute to tree mortality. It introduces a “drought memory” term as a predisposing factor, capturing the effects of long-lasting drought conditions (Marano et al., 2024). In addition, it incorporates an inciting factor that represents drought duration, as well as spring and autumn soil moisture deficits that can limit bud break and carbon reserve replenishment for the subsequent year. This framework acknowledges that a series of dry years can intensify mortality risk under prolonged summer drought and early- or late-season soil moisture deficits, conditions that can be loosely compared to the onset of hydraulic failure—though neither carbon starvation nor hydraulic failure is explicitly modeled.

LPJ-GUESS did not show any significant increase in mortality rate following the consecutive drought events in 2018 to 2020. The simulated mortality rate remained within a range similar to the years without drought, showing a marginal increase after 2018, peaking at 0.28% in 2019. This slight increase in tree mortality is linked to the implemented growth efficiency-related mortality, which accounts for tree mortality due to poor growing conditions, such as water or nutrient availability and shading. However, it is heavily influenced by shading class parameters, which are specific for different plant functional types, and which represent mortality due to shading rather than catastrophic events like climate extremes.

Consequently, shade-tolerant plant functional types typically exhibit lower mortality rates, reflecting their capacity to endure low-light conditions with reduced growth efficiency, but not their resilience to extreme climatic conditions and their effects. Thus, growth efficiency related mortality was not sufficiently sensitive to capture the impact of drought during the consecutive drought years of 2018 to 2020 when compared to observed tree mortality rates.

FORMIND showed comparable mortality rate values in drought years as in years without drought. This is due to the fact that the parameterization used for this simulation study used a background and a tree size-dependent mortality approach. The smaller the tree, the higher the tree mortality. Long-term data and yield tables have been used to calibrate this mortality concept and the climate-dependent tree growth (Bohn et al., 2014). As a result, spruce growth is reduced during a drought, but the selected mortality approach has hardly any effect on spruce mortality. The only small effect is that if the trees grow more slowly or not at all (in drought years), they remain in a smaller size class and therefore at a higher mortality level compared to trees that grow (in non-drought years).

3-PG-Hydro does not incorporate a process-based drought mortality model and therefore it was expected to not show any mortality response. Although 3-PG-Hydro contains process-based self-thinning and age-dependent mortality, no mortality was simulated due to the stand density and age not exceeding the thresholds for mortality. Nevertheless, water stress reducing forest productivity was observed in the drought years. This process is well implemented in 3-PG-Hydro by reduction of NPP relative to soil water content in the root zone and haltering productivity with water content falling below the wilting point.

While the models simulated the long-term average spruce mortality quite well in years without severe drought (Fig. 1A), the models generally failed to reproduce large-scale mortality after several consecutive years of severe drought during the years 2018–2020 (Fig. 1B). Besides mortality, we investigated how the productivity of forests changes during drought years. As all forest models use approaches of limited tree growth during drought conditions, we assume that we can observe reduced simulated productivity in the drought years 2018–2020. We therefore analyzed the annual change in the stand basal area as a proxy for stand productivity and correlated this with the drought index SPEI (Fig. 2). Comparing the stand basal area change with the SPEI should result in a positive correlation, i.e. the wetter it is, the better the stand growth. All models reacted to drought events with stand growth depressions showing a reduced basal area change as soon as a drought event occurred (Fig. 2C). However, the drought response varied in intensity between the models. Especially FORMIND and GOTILWA + showed a clear positive correlation between the drought index SPEI and basal area change.

In summary, we have shown that the models show acceptable performance in simulating long term trends of a spruce forest under normal climate conditions. If multi-year droughts occur, tree growth is reduced to varying degrees in all mod-

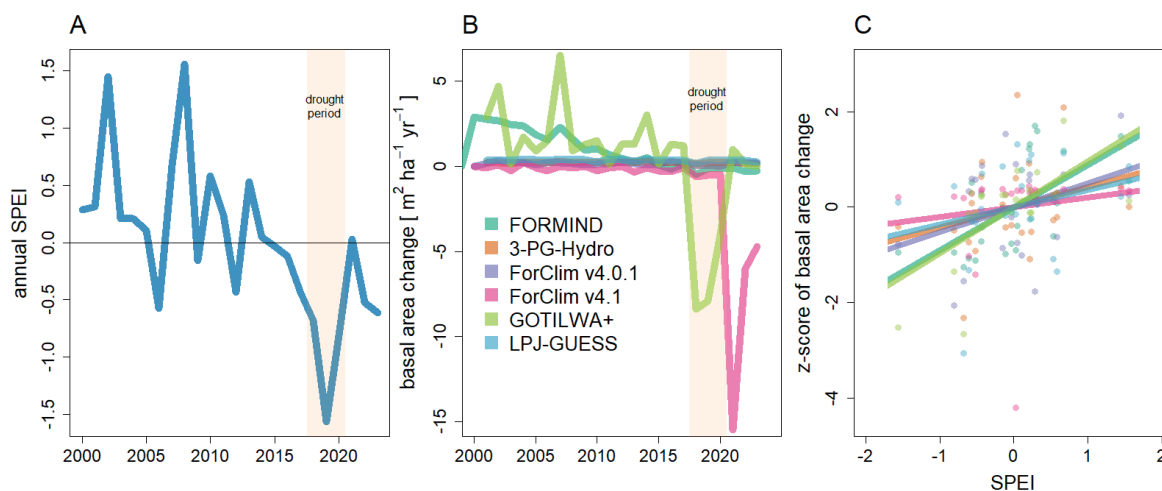


Fig. 2: Comparison of simulated forest growth with drought index SPEI. The calculation of the SPEI and the explanation of the climate data (here ERA5-Land) can be found in the supplementary information S5 and S3. (a) Annual drought index SPEI calculated from the local ERA5-Land values. Negative values indicate years drier than the long term average. The orange zone indicates the years with extreme drought conditions. (b) Development of the basal area change of the simulated spruce forest stand for each model. The change in the basal area results from growth processes, regeneration and mortality. (c) Comparison of the z-score of the basal area change with the SPEI for each model run. The z-score indicates how far a data point is from the model-specific mean of the basal area change. The lines indicate model-specific linear trends. A positive slope indicates that the basal area change decreases as it becomes drier.

els, but they all have their challenges in reproducing spruce mortality. Although we have only shown model simulations for spruce forest as an example, the model algorithms would likely lead to similar results also for other tree species in Central Europe. Thus, there is a great need to rethink and revise the representation of mortality processes in these models, with the aim of achieving more accurate model predictions under climate change.

Perspectives for revising forest models to represent massive tree mortality

Forest models are generally better at simulating the growth process than the mortality process (Bugmann et al., 2019; Bugmann & Seidl, 2022). Most forest models (but also land surface models and DGVMs) are designed to simulate – to a greater or lesser degree – the decline of tree growth or productivity, as this is explicitly formulated. What these models do not seem to adequately simulate are mortality patterns and vegetation dynamics during a multi-year drought and in the post-drought period: our model comparison study for the Harz Mountain region in Germany showed that the forest models did not satisfactorily reproduce large-scale spruce mortality events after several years of drought combined with pests and diseases. The observed mortality events after the 2018–2020 drought are likely due to both drought and bark beetles. The fact that the models cannot accurately reproduce this mortality event is not really surprising, as most of them do not incorporate drought-induced mortality triggers or insect attacks. We therefore propose four perspectives that should be considered in future model developments in order to better reflect such forest damages and thus provide more reliable projections for the future.

Perspective 1: Integration of process-based modelling approaches into drought-induced mortality formulations

Integrating process-based representations of drought-related tree mortality into dynamic forest models can enhance our understanding of the mechanisms leading to tree stress, but also the influence of climate, soil, and plant traits on species responses to climate extreme events. Potentially, such integration can help reduce uncertainties in model predictions by providing a more comprehensive assessment of climate change on forest dynamics (McDowell et al., 2008; McDowell, 2011; McDowell et al., 2013). Yet, both the interplay between processes and the level of detail of process resolution are not straightforward to determine, as explained below.

Prolonged growth reduction is often considered as a predisposing factor leading to tree mortality (Berdanier & Clark, 2016; Cailleret et al., 2017; Neycken et al., 2022). In this context, the concept of reduction factors is being used in process-based forest models that are linked to growth or productivity, and these encompass diverse approaches such as Liebig's law of the minimum (Liebig, 1841; Kienast, 1987) or fuzzy logic (Seidl et al., 2005).

Long-lasting growth reduction alone is however not sufficient to explain abrupt tree decline, as legacy effects of past stress events (e.g. previous droughts) also contribute to weaken trees and predispose them to future stress (Manion, 1981). In this sense, the way these mechanisms are implemented within the model structure is crucial to ensure that the model not only captures and utilizes historical stress signals (e.g., past water stress), but is also able to preserve part of the stress signal in a memory term that influences plant responses to future stress. While some models accurately capture long-term carbon storage in the vegetation pool (Fischer et al., 2016; Yan et al., 2019), they struggle to retain soil water

deficit information (Anderegg et al., 2013; Fowler et al., 2021) – as they were developed primarily to simulate carbon (and wood) stocks or species composition trends.

It is essential to recognize that interactions among various processes, such as carbon starvation or hydraulic failure, are as crucial as the processes themselves, particularly in the context of drought-induced mortality (O'Grady & Mitchell, 2015). In this context, Manion's decline-disease theory (Manion, 1981) illustrates that tree mortality results from a combination of predisposing, inciting, and contributing factors. This intricate interplay is often overlooked by process-based forest models, which tend to oversimplify tree death by emphasizing certain pathways over others (Wang et al., 2012).

Interestingly, both GOTILWA+, the only model in our study that attempted to represent this interplay of factors physiologically, and ForClim v4.1, which applied a non-physiological approach, got close to capturing the observed mortality pattern. However, they either under- or overestimated the magnitude or the onset of tree mortality. The reason other models were not able to reproduce high mortality rates may be that they emphasize either predisposing or inciting factors, but not both. In addition, some models do not have algorithms to capture drought-related mortality, while no models evaluated represent biotic effects such as bark beetle outbreaks. By carefully balancing model complexity with computational manageability and integrating predisposing and inciting factors schemes into process-based representations of drought-induced tree mortality, forest models can improve their accuracy in simulating compound extreme events such as drought related tree mortality.

Perspective 2: Modeling ecophysiological processes in response to drought

Incorporating species traits and hydraulic behavior is challenging due to increased model complexity, often resulting in more parameters reliant on empirical thresholds linked to system shifts during extreme droughts (Wang et al., 2012). These traits encompass various physiological and morphological characteristics that influence a tree's ability to withstand periods of limited water availability (McDowell et al., 2008; Serra-Maluquer et al., 2022). Key traits include drought tolerance (i.e., a tree's ability to survive and maintain functionality during prolonged dry conditions) and hydraulic behavior, which pertains to how trees regulate water transport and maintain water status under drought conditions (McDowell, 2011; McDowell et al., 2013). Trees are often classified as either isohydric or anisohydric, representing contrasting water-use strategies during drought (Sperry et al., 2002; Martínez-Vilalta et al., 2014). Isohydric trees maintain stable leaf water potential by closing their stomata early in response to drought, conserving water but preventing also the photosynthetic uptake of CO₂ – and therefore carbohydrate production – in order to maintain plant functions. Prolonged periods of drought can therefore lead to the depletion of mobile carbohydrate pools due to carbon starvation. Conversely, anisohydric trees allow greater fluctuations in leaf water potential, keeping stomata open longer for continued photosynthesis and growth, but increasing the risk of hydraulic failure due to

embolism. Put simply, plants can starve (carbon starvation) or die of thirst (hydraulic conductivity failure) during prolonged drought. However, many species display intermediate behaviors or switch strategies depending on environmental conditions, such as soil texture (Martínez-Vilalta & Garcia-Forner, 2017; Brinkmann et al., 2019) which are also often not represented by forest models. Carminati & Javaux (2020) emphasize that soil hydraulic conductivity significantly influences stomatal regulation and drought responses more than xylem vulnerability does, altering root water uptake and impacting plant water status and drought resilience. Arend et al. (2021) provide evidence that hydraulic failure is the primary driver of drought-induced mortality in Norway spruce. During the 2018 drought, dying adult trees showed a rapid, nonlinear decrease in xylem pressure, resulting in a complete loss of xylem hydraulic conductance, while severe depletion of non-structural carbohydrates, indicative of carbon starvation, was observed in both dying and surviving trees.

Models aiming at simulating drought-induced tree mortality should thus integrate detailed water and carbon balance calculations including the risk of mortality due to hydraulic failure and carbon starvation. In addition to direct mortality from drought as an inciting stress factor (Manion, 1981), water stress also plays a key role in increasing the risk of infestations in bark beetle outbreaks (Temperli et al., 2013; Seidl & Rammer, 2017).

The threshold value for the onset of drought-induced mortality depends on the anatomy, morphology and ecophysiological strategies of the trees and their water transport system, which are adapted to the climatic conditions of their distribution area (Carnicer et al., 2013). Nevertheless, ongoing climate change-induced changes are too abrupt for many tree species and adaptation to changing climatic conditions within the lifetime of a tree will most likely be difficult (Trumbore et al., 2015). In summary, an improved representation of water stress can enhance model predictions, particularly when accounting for additional contributing stress factors, such as insect outbreaks, that influence drought-related tree mortality.

Another critical issue is how to include carbon starvation as a predisposing factor of death and how detailed the photosynthetic and stomatal processes need to be captured in the models to simulate hydraulic failure. Only few models are able to capture the very complex process of hydraulic failure and to investigate such questions as LPJ (Hickler et al., 2006), SurEau (Cochard et al., 2021) and MLCan (Quijano et al., 2013). Even fewer capture the full interplay of hydraulic failure, carbon starvation and tree mortality. GOTILWA + and MEDFATE, for instance, incorporate the mechanisms of carbon starvation and hydraulic failure as drivers of mortality (Nadal-Sala et al., 2017; Sperlich et al., 2020; De Cáceres et al., 2022).

To improve predictive ability of forest growth models regarding drought-induced mortality, a mechanistic representation is necessary. However, the detail of the processes should be not too extensive to facilitate integration in existing models. A simple approach to approximate carbon starvation is implemented in the iLand model, where stress-related mortality is related to declining carbohydrate availability through a stress

index. This index increases as turnover demands for foliage, fine roots, and reserves exceed available carbon, ultimately leading to tree death when critical thresholds are reached (Seidl et al., 2012). To implement the processes leading to mortality due to hydraulic failure in models, we propose a simple approach based on Choat et al. (2018), Cochard et al. (2021) and Torres-Ruiz et al. (2024). Relative to the duration of the soil hydrological drought (water content below the wilting point), the percentage loss of hydraulic conductance (PLC) increases exponentially from a critical point. This critical point is reached when growth processes (e.g., photosynthesis) stop and stomatal conductance is lost following a complete stomatal closure. The slope of the PLC curve is additionally influenced by the magnitude of vapor pressure deficit. Mortality sets in after a specific threshold of PLC is exceeded. This threshold value (point X_1) and the critical duration of the drought (point X_2) must be parameterized specifically for each plant species (Fig. 3).

The aim of this perspective is to implement ecophysiological processes in a simplified manner to reduce modelling complexity. With the simple approach presented here, forest models could easily implement the processes leading to mortality due to hydraulic failure and potentially better capture drought-induced tree mortality.

Perspective 3: data-driven approaches of tree mortality modeling

Statistical regression analysis is the classical way for investigating cause-effect relationships. For robust statistical inference, large amounts of observational data are required. In the case of tree mortality, these observations concern living and dead trees. Compared to the number of living trees there are only a few dead trees per year, so tree mortality is a rare event. Thus, only systematic long-term monitoring programs with large plot networks and annual reporting, like ICP Forests (Michel et al., 2023), can provide sufficient tree mortality data. In addition, the observed tree losses need to be classified according to their causes such as planned harvest, thinning operations, competition (self-thinning) and damages by abiotic or biotic agents to be able to model the different forms of mortality (Lech & Kamińska, 2024). Such data can be filtered for different categories and combined with potential environmental drivers as independent variables to derive statistical relationships with the dependent variable, i.e. the probability of a tree to die. Potential drivers come from the domains of climate, topography, soil, land cover, pollution, forest structure, or pest population dynamics, and may include individual tree attributes such as age, past vitality and competitive situation (Taccoen et al., 2022; Neumair et al., 2022; George et al., 2022; Tymińska-Czabańska et al., 2022; Knapp et al., 2024). During the fitting procedure, the most important predictors are identified to achieve accurate predictions with a parsimonious predictor set.

Logistic regression has often been the method of choice for modeling mortality, as it is designed for fitting binary dependent variables (surviving vs. dying trees) and returning the probability for the occurrence of an event (mortality rate). While non-parametric methods such as decision trees could

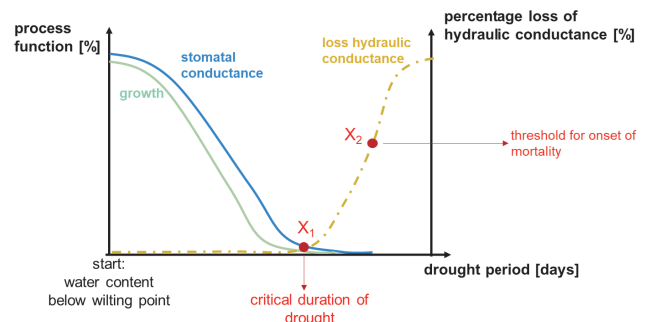


Fig. 3: Schematic representation of the processes that lead to tree mortality due to loss of hydraulic conductance. The diagram was adapted from Choat et al. (2018) and Torres-Ruiz et al. (2024).

be used for the same purpose, logistic regression has some advantages in incorporating the statistical relationship into process-based vegetation models. Firstly, the logistic regression equation is a generalization of simple linear regression and it is straightforward to formulate this equation in any programming language and to transfer the fitted coefficients from the statistical software to the vegetation model. Secondly, it is a smooth continuous function with a certain ability to extrapolate beyond the training data range, a characteristic that would be very desirable in the face of climate change. It should be mentioned, however, that predictions beyond the calibration range have limited predictive capability when projecting into novel conditions as their functional shape has not been constrained by data and thus need to be taken cautiously (Thripleton et al., 2021). Consequently, there is a high degree of uncertainty in predictions. In the meantime, models could benefit from revised regression approaches that incorporate data covering new climate ranges, for example by incorporating observations of climate change effects on growth and mortality from climate change experiments.

A applications of empirical models of drought mortality in Germany (e.g., Knapp et al., 2024; Anders et al., 2025) have been found to be relatively effective in reproducing the complex interaction of multiple stressors (e.g., hydraulic failure, carbon starvation, biotic factors) in spruce-dominated forests. For instance, by considering only a few selected climatic predictors Anders et al. (2025) captured the drought-driven mortality of spruce trees and the impact of biotic stressors (e.g. Norway spruce mortality due to bark beetles). Also Knapp et al. (2024) achieved a high cross-validated accuracy for the mortality of spruce trees in Germany, including more environmental predictors such as soil conditions and proximity. These examples show the potential of further explorations, e.g., multi-species approaches, in which empirically calibrated mortality models could be a suitable alternative to replace the inflexible mortality parameterisations in process-based models used to date.

The complexity of mortality processes and limited, potentially biased sample data introduce significant uncertainty in these models. To improve accuracy, further research is needed to refine empirical mortality algorithms, enhance data collection methods, optimize model calibration, and identify key predictor variables for inclusion in models.

Hence, we see three use cases for statistical models in the context of forest mortality modeling:

1. Spatio-temporal prediction purely based on statistical models. Using wall-to-wall predictor datasets covering the past climate and future climate scenarios, the statistical model itself is a powerful prediction tool for forecasting mortality rates for the coming decades. For example, based on Germany-wide high-resolution mortality predictions (Knapp et al., 2024), we were able to extract the mean spruce mortality time series for the Harz Mountains alongside 100 local trajectories from within the region (Fig. 1). These trajectories can serve as a benchmark for the process-based models (Fig. 1).
2. Statistical mortality components in process-based vegetation models. Such approaches can serve as temporary solutions as long as process-based models (cf. perspective 1) are unable to accurately predict historical tree mortality events using mechanistic approaches. In addition, process-based models can be used to further assess the impact of tree mortality on forests, as they simulate vegetation dynamics such as reproduction, regeneration, growth, management options and species turnover (Anders, et al., 2025). As shown by Hülsmann et al. (2018), Thrippleton et al. (2021) and Anders et al. (2025), a successful integration of empirical mortality equations in process-based models is possible in principle, but the selection of the empirical model (e.g., predictor variables) has to be made cautiously. Once process understanding has increased, the empirical model components can be replaced by mechanistic model components.
3. Statistical predictions for process calibration: Process-based models require data to calibrate them. In the case of mortality, field observations are sparse and by themselves provide a very limited calibration data resource. Statistical predictions can enhance the amount of available data by many orders of magnitude. Once the processes in the models have proven to reproduce patterns in the known range of environmental conditions, they are our best chance to correctly predict system behavior under novel conditions.

Beyond classical statistical approaches, Artificial Intelligence (AI), or more specifically machine learning (ML) has emerged as a powerful tool for modeling and categorizing drought-related forest mortality. For instance, Cho et al. (2023) explored various machine learning techniques to analyze tree mortality and growth reduction, using climatic and ecophysiological predictors. According to Cho et al. (2023) machine learning algorithms outperformed conventional multiple linear regression, with random forest showing the highest overall accuracy for tree mortality predictions. Da Rocha et al. (2018) and Reis et al. (2018) used artificial neural networks to predict tree mortality in Brazilian rainforests. However, these models demonstrated low predictive ability in predicting tree mortality, emphasizing the need for further refinement of these novel modeling techniques. In addition, the impact of bark beetle outbreaks on tree mortality, an important secondary effect of prolonged drought, has been extensively studied (Hlásny & Turčáni, 2013; Fassnacht et al., 2014; Rammer & Seidl, 2019). Notable work includes also the use of machine learning algo-

rithms such as artificial neural networks to predict bark beetle-induced fellings, and support vector machines to detect bark beetle-affected areas using hyperspectral remote sensing data (see Perspective 4 for more details on representing biotic damaging agents in forest models).

The listed AI applications are primarily stand-alone and focus almost exclusively on predicting mortality without considering its repercussions on forest productivity, stand structure, and recovery after disturbances. In contrast, process-based forest models are adept at capturing dynamics such as regeneration and growth, but they typically fail to incorporate drought-induced tree mortality into their simulations. To leverage the benefits of both methods, the literature suggests hybrid models, i.e. by integrating AI with process-based models (Reichstein et al., 2019; Zhang et al., 2021; Horvath et al., 2021; Cho et al., 2023).

To date, hybrid approaches have been only partially explored, for instance, using machine learning to refine initialization parameters (Li et al., 2023) or to generate species distribution maps (Horvath et al., 2021), whereas both approaches use ML as a preprocessing step in order to run the global vegetation models. In the future, as machine learning algorithms are increasingly being used with remote sensing data to produce large-scale tree mortality maps that are regularly updated (Fassnacht et al., 2014; Schiefer et al., 2023), we emphasize that these maps provide new opportunities nudging forest models and global vegetation models, i.e. adjusting forest dynamic simulations to ML-based mortality detections even during model runtime (towards digital forest twins). While hybrid modeling holds promise, its application faces challenges. Foremost the substantial computational demands of machine learning often limit its practicality for large-scale forest simulations as carried out in DGVMs. Future studies therefore might address the increased computational demands, i.e. through advancements in high-performance cluster computing.

Perspective 4: Representation of biotic damaging agents in forest models

Biotic pests are of particular importance for forest development. They are highly sensitive to global warming and are invading forests as alien pests and pathogens, sometimes with dramatic ecological and economic consequences. These biotic disturbances are usually associated with periods of drought or storms and can change large forest landscapes in the long term, as has already been observed in the past in the Bavarian Forest or currently in the Harz Mountains. In simulating forest dynamics, biotic disturbances are often ignored or only a few agents are considered (Honkaniemi et al., 2021). Most forest models currently focus solely on abiotic factors.

Thanks to an increasing number of remote sensing applications, we know more and more about where and when forest disturbances occur and can analyze their patterns (Senf & Seidl, 2021). However, it is often not possible to differentiate between the causes of disturbance, or only very broad classes of causes are described (e.g. <https://forestpaths.eu/>, Viana-Soto & Senf, 2024). This is mainly due to a lack of ground-

truth data. This lack of information, but also the partially incomplete understanding of processes, makes it difficult to integrate biotic factors into forest models.

Initial attempts have been made to model bark beetle dynamics in vegetation models. Bark beetle infestations can be simulated across various spatial scales, with a growing number of process-based infestation models developed over the past two decades (Huang et al., 2020). These models have evolved mainly in two directions: i) spatially explicit agent-based models of bark beetles, which allow detailed simulations at the level of individual trees and beetles (Kautz et al., 2014; Honkaniemi et al., 2018). ii) the aggregated integration of bark beetle dynamics into vegetation dynamics models like forest landscape models and dynamic global vegetation models (Landry et al., 2016; Seidl & Rammer, 2017). While agent-based models provide detailed representations of processes such as dispersal and tree defense but are only locally applicable, integrated models offer a broader scope but with less detailed process representation.

A successful model example is BITE (Biotic disturbance Engine), a process-based approach to simulating biotic forest disturbance agents from fungi to large mammals (Honkaniemi et al., 2021). This model already integrates six different biotic disturbance agents (*Heterobasidion annosum*, *Hymenoscyphus fraxineus*, *Lymanthia dispar*, *Anoplophora glabripennis*, *Capreolus capreolus*, *Mammut americanum*). The simulation of biotic disturbance agents entails an examination of the potential habitat of the animal or pathogen, its introduction, spread, colonization, the population dynamics and its impact on the vegetation. Each of these processes is parameterized based on available data, which also represents a limitation in the transfer to other regions and underscores the lack of data issue.

The iLand landscape model has already incorporated a submodule that addresses the European spruce bark beetle, based on the BITE model (Rammer et al., 2024). The probability of bark beetle outbreaks varies across regions and is influenced by the local climate. A phenology-based process model is employed to simulate the dynamics of the beetle population. This model takes into account the thermal requirements for development and determines the number of generations and sister broods that the insect can complete per year. The success of host tree colonization is contingent upon the host tree's capacity to defend itself, which is indirectly dependent to the effect of drought. The spatial dispersal of the beetles is explicitly simulated. In the event of successful colonization, the tree will inevitably perish. The overwintering of the beetles is a function of their life stage and the minimum winter temperatures. The fitness of the beetles declines with the duration of an outbreak, resulting in an increase in mortality and a local collapse of the populations after a few years.

Furthermore, algorithms based on artificial intelligence are also used to map biotic influencing factors (see also perspective 3). Notable contributions include machine learning algorithms such as artificial neural networks to predict bark beetle induced fellings (Hlásny & Turčáni, 2013) or the use of support vector machines to detect bark beetle-induced mortality from hyperspectral imagery from remote sensing

(Fassnacht et al., 2014). Furthermore a study by Rammer & Seidl (2019) utilized deep learning, which can be described as an artificial neural network with multiple layers, to predict both the short-term infestation risks at the local scale and the long-term outbreak dynamics at the landscape level.

Population dynamics of biotic agents are rarely studied in the context of drought effects, but could be incorporated into forest models, for example with the BITE model. The challenge is to link these two model worlds (detailed bark beetle models vs. forest or landscapes models), which sometimes have very different spatial and temporal scales. In addition, the forest microclimate is a very important driving factor for the spread of insects and diseases, but has not yet been fully considered in forest models (Kautz et al., 2013; Seibold et al., 2016; Dillon & Meentemeyer, 2019; Sallé et al., 2021).

Synthesis and Conclusion

Modelling forest dynamics, particularly in the context of drought-related tree mortality, remains a major challenge due to the complexity of ecological interactions, limited empirical knowledge and the consequent lack of comprehensive mechanisms in dynamic forest models. While current models perform well in simulating tree growth, their ability to represent mortality, especially due to drought events, is limited. This discrepancy highlights the urgent need for methodological improvements.

The perspectives proposed above provide a roadmap for addressing this issue. First, incorporating eco-physiological processes, including species-specific hydraulic and carbon strategies, may be critical for simulating the nuanced responses of trees to drought. Second, statistical regression models can be used to complement these efforts by providing robust empirical relationships for mortality under current conditions that may be applicable, at least to some extent, under global change conditions. In the absence of fully-fledged physiological approaches, their integration into process-based models allows for more accurate representations of mortality. Third, hybrid approaches that combine artificial intelligence and process-based models hold promise for revolutionizing mortality modeling. AI-driven techniques can identify patterns and refine parameters, while process-based models provide the structural framework to simulate long-term forest responses to climate change. Finally, biotic disturbance agents such as bark beetles are pivotal in forest dynamics but are inadequately captured in current models. Advances in modeling pest dynamics underscore the potential for integrating biotic factors with abiotic stressors like drought.

However, we cannot specify which of the proposed paths is the most promising for the further development of forest models, as this depends on many factors. Firstly, the availability of empirical data to model mortality processes is often a challenge. Further measurements (e.g. sap flow), but also remote sensing data of mortality patterns can be helpful. In addition, the processes that led to tree mortality events are often unclear or result from a complex interplay of abiotic and biotic factors. Another challenge is the adaptability of models. Not all of the ideas presented here can be implemented

in dynamic forest models, as this requires a certain flexibility and modularity of the models. Finally, the actual scientific question, which determines the necessary level of detail of the mortality approaches, is paramount and will dictate both what is needed and what is possible in terms of the inclusion of process representations. This means that not every modelling study investigating forest dynamics under drought conditions requires the highest level of detail in modelling eco-physiological processes – even simple modelling approaches can provide meaningful simulation results.

In conclusion, significant advances in forest modelling are needed to better predict the future of forests under climate change. The integration of process-based and data-driven mortality approaches will improve our ability to capture drought-related tree mortality. Incorporating biotic agents and ecophysiological traits into forest model structures, along with hybrid AI approaches, has the potential to reduce prediction uncertainties and provide a more holistic representation of forest dynamics. Ultimately, improving forest models to reflect the interplay of mortality drivers is not only a scientific imperative, but also a cornerstone for informed forest management and policy-making in the face of accelerating climate change.

Conflicts of interest

The authors declare that they do not have any conflicts of interest.

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Supplementary Information

S1: Model description and simulation setting

Five models (ForClim, 3-PG-Hydro, LPJ-GUESS, GOTILWA+, and FORMIND) were used for this simulation study, which are described below. With all models, a spruce-dominated forest of the Harz Mountains under the climatic conditions of the years 2000 to 2023 was simulated. The same forest inventory data was used by all models to initialize them. We run simulations from 2000 to 2023 using climate data from ERA5.

ForClim

This study employs two versions of the individual-based forest process model ForClim, namely versions 4.0.1 and 4.1 (Marano et al., 2024; Huber et al., 2020). ForClim is particularly adept at simulating forest succession on small patches (gaps) typically ranging from 400 to 1000 square meters (Bugmann, 1994). ForClim is a forest gap model (Botkin et al., 1972; Bugmann & Seidl, 2022) that focuses on four key processes governing forest dynamics: tree establishment, growth, mortality, and light competition among trees within a forest patch. These processes collectively determine the behavior of individual trees and the forest stand. ForClim incor-

porates environmental factors such as temperature and soil water availability, which impact forest dynamics at the tree level. They play a pivotal role in constraining tree growth and increasing the risk of mortality. Each tree species in ForClim is characterized by functional traits, including shade tolerance, frost resistance, drought resistance, and many others. Model outputs are calculated annually for each individual tree and can be aggregated to analyze forest attributes at the species and stand levels.

ForClim's modular structure features a number of submodels to capture forest dynamics. The weather submodel offers two options, both of which were employed in this study.

1. Stochastic weather generation (ForClim v4.0.1): This method randomly samples monthly climate parameters (precipitation totals, mean temperatures) from their long-term statistics (i.e., means and standard deviations). Thus, each forest patch is characterized by a unique weather time series, thus enabling it to capture both intra- and inter-annual variability. The model employs a simplified soil water bucket concept, assuming homogeneous soil properties across all simulated patches. Thus, spatial heterogeneity of soil moisture is introduced by the patch-specific sampling of weather variables.
2. Weather time series (ForClim v4.1): This approach employs actual monthly weather data (precipitation sum, mean temperature) in time series format to reproduce historical weather events. To take into account spatial heterogeneity, this model version incorporates spatially distributed soil properties, while monthly weather is uniform across patches. Following Manion's Decline-Disease theory (Manion, 1981), ForClim v.4.1 explicitly accounts for non-linear interactions among multiple climatic stressors leading to tree mortality, by distinguishing predisposing and inciting factors which affect both the growth reduction and stress-induced mortality formulations (Marano et al., 2024).

ForClim offers a diverse set of model variants, each with a distinct formulation for tree establishment, growth, and mortality. They account for uncertainties in the model structure (Huber et al., 2021). ForClim can be accessed via the following link: <https://fe.ethz.ch/en/research/stand-and-landscape-dynamics/models.html> (last accessed May 1, 2024).

Simulation settings: To initialize the forest state in ForClim, we utilized the inventory data representing a 10-hectare pure Norway spruce (*Picea abies*). This data was processed to determine the number of patches (simulation units in gap models) required to cover the forest area, with each patch measuring 500 m². To ensure a representative distribution of trees across the simulated forest, the inventory data was scaled and trees were randomly assigned to each of the 200 patches. Finally, a structured table was generated, containing the species name and diameter at breast height (DBH), and the assigned patch number for each tree. This table served as the initialization file for the ForClim simulation, defining the initial state of the forest. The spruce trees were simulated from a minimum DBH of 1.27 cm. Nevertheless, only trees with a DBH of 7 cm or more were included in the subsequent analysis. The simulations were run for a period of 24 years,

from 2000 to 2023. Furthermore, the latitude of the stand (51.73°) was included in the parameterization of the model.

Soil properties, including field capacity (22.9 cm), permanent wilting point (5.7 cm), and soil depth (100 cm), were employed to derive pertinent parameters, such as available water capacity (ForClim v4.0.1: $kBS = 17.2$ cm; ForClim 4.1: $kBS_{mean} = 9.0$ cm; $kBS_{min} = 8.5$ cm). The available nitrogen ($kAvN$) was set to $100 \text{ kg ha}^{-1} \text{ yr}^{-1}$, assuming a negligible role of nitrogen limitation in the area.

It is important to remark that for the current simulation study the choice of the available water capacity, as well as the climatic data employed, has an impact on the simulation outcomes. In a first simulation study, the kBS values for ForClim v.4.1 were set to respectively 17.3 cm and 25 cm for the minimum and mean and German Weather Service ‘DWD’ data at 1 km resolution have been employed (Fig. S1, DWD Climate Data Center (CDC) version v19.3, DWD = Deutscher Wetterdienst)

In this case, the model kills trees already in the year 2019 but fails to reproduce the subsequent mortality pattern in the years 2021–2023.

Simulations conducted with ForClim v4.1 using the DWD dataset resulted in an earlier onset of the strong mortality surge, highlighting the sensitivity of the model to specific weather data inputs. This also underscores the large influence of soil properties in the model. The observed discrepancies between simulated and observed mortality peaks after 2018 suggest that uncertainties in driving data, such as weather and soil parameters, contribute to the model limitations in capturing real-world phenomena. This observation also extends to GOTILWA+, where variations in driving data could potentially lead to different peaks in the mortality simulations.

Two approaches were employed to account for variability in the climate data. The first approach involved the use of a

weather generator. The weather time series approach relies on the provision of the original time series aggregated at the monthly time step for the period of interest, hence 2000–2023, and at least 30 years of historical time series. This necessary step enables the model to calculate a site index, which depends on both degree days and drought conditions. For both methods, we employed ECMWF ERA5-LAND reanalysis data aggregated at the monthly time step for the periods January 2000 to December 2023 for the weather generator and January 1950 to December 2023 for the weather time series. For the latter approach, the ERA5-LAND reanalysis data were downloaded via Google Earth Engine:

script: <https://code.earthengine.google.com/93b5c5eafc1699565137e7a4c2890876>.

A detailed description of the ERA5 product can be found at https://developers.google.com/earth-engine/datasets/catalog/ECMWF_ERA5_MONTHLY_MONTHLY_AGGR#description.

FORMIND

The forest model FORMIND is an individual- and process-based forest gap model (the 2022 model version was used here; Fischer et al., 2016). It simulates the growth dynamics of all trees within a forested area (here 10 ha) divided into patches with a size of $20 \text{ m} \times 20 \text{ m}$. The main processes in FORMIND that are calculated at each time step for each tree individually are tree growth, establishment, and mortality. Trees within one patch compete for light, space and soil water.

One main driving force of tree growth is the incoming light, which is defined in the model as the photosynthetic photon flux density. The productivity of a tree is influenced by its crown size as well as by the available light, the accessible soil water content, and the air temperature. The light availability of a tree can be reduced by shading from larger trees in the same patch. The productivity rate and biomass gain of a single tree are calculated as the difference between photosynthetic production and respiratory losses.

In FORMIND, trees can die for several reasons, such as age (i.e., tree size-dependent mortality), competition for space, or damage from larger trees that fall. The parameterization used takes into account species-specific tree mortality, which is a function of stem diameter. Species-specific mortality parameters are taken from Bohn et al. (2014).

The soil water content of each patch is calculated continuously and is mainly driven by precipitation, interception, evapotranspiration, and runoff. To simulate diverse climatic conditions, FORMIND necessitates a daily climate data input comprising daytime mean PPFD, daily precipitation, the daytime mean of air temperature and the day length. Consequently, the impact of fluctuating climatic conditions on the carbon balance at both the tree and ecosystem levels can be evaluated, as well as the aboveground biomass and basal area.

A FORMIND parametrization (Bohn et al., 2014) developed to simulate European tree species in the temperate zone is employed to simulate spruce forests. This parametrization has been previously validated through successful application

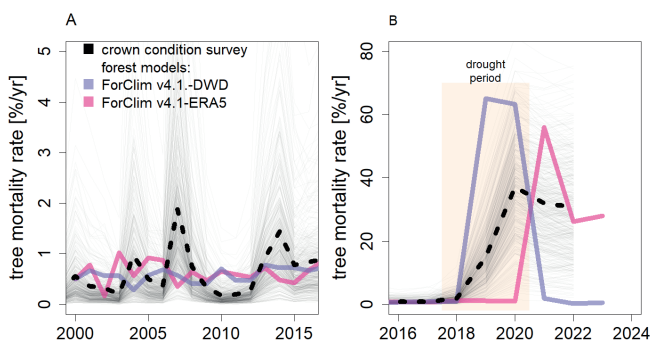


Fig. S1: Spruce mortality in the Harz Mountains from 2000 to 2023. The simulated spruce mortality of ForClim v.4.1 using two different climatic data sources, namely DWD and ERA5 reanalysis (colored solid lines), is compared with the estimated spruce mortality based on the annual national crown condition survey (black dashed line). A) Simulated tree mortality for the non-drought period 2000–2016. B) Simulated tree mortality after several years of drought 2018–2020. Please note the different scaling of the y-axis for A) and B). The orange zone indicates the years with extreme drought conditions 2018–2020. The black dashed line is the mean mortality across all forest stands in which spruce occurred in the Harz Mountains and thus serves as a reference for spruce mortality.

in numerous simulation studies conducted in Germany and has also been tested against eddy covariance measurements (Bohn & Huth, 2017; Rödig et al., 2017; Fischer et al., 2019; Holtmann et al., 2021).

3-PG-Hydro

3-PG-Hydro is an upgraded version of the process-based model 3-PG (Landsberg & Waring, 1997) that was developed to represent important hydrological processes. 3-PG is a stand-scale process-based model that includes five physiological sub-models simulating the processes of light absorption, biomass production, water balance, biomass allocation and mortality (Landsberg & Waring, 1997). 3-PG has been applied globally for decades in the context of forest growth simulations and management, performing well under various conditions (Gupta & Sharma, 2019). Moreover, 3-PG showed well suitability for simulations in Central Europe (Augustynczyk et al., 2017; Nölte et al., 2020; Forrester et al., 2021). The here applied upgraded version 3-PG-Hydro integrates a detailed soil-water model that can simulate infiltration and percolation processes on a daily time step thus making 3-PG-Hydro a tool for analysing forest and water interactions (Yousefpour & Djahangard, 2021). Hereby, drought conditions impact forest productivity. 3-PG-Hydro cannot simulate mortality caused by biotic or abiotic disturbances in a process-based manner. However, annual stress-related mortality can be integrated as an empirical function of age but we did not apply this in the modelling setup.

For initialization, 3-PG-Hydro requires the following data on stand scale: the mean age (years), the stem number (trees per hectare), mean diameter at breast height (cm), soil parameters (water retention curve, coarse fragments and soil depth) and a set of species-specific parameters. The species parameters for Norway spruce were taken from Forrester et al. (2021).

GOTILWA+

GOTILWA+ (Growth Of Trees Is Limited by WAtER, <http://www.crea.uab.es/gotilwa/>) is a detailed process-based biogeochemical model that simulates tree growth, and the associated carbon and water fluxes to investigate effects of tree stand structure, management interventions, soil properties, water stress and climate change (Gracia et al., 1999; Keenan et al., 2009; Nadal-Sala et al., 2019; Sperlich et al., 2020).

GOTILWA + simulates monospecific forests of evergreen broadleaved or conifers and deciduous species which are distributed in diameter classes – this allows the coupling with economic model (Sperlich et al., 2024). A management module regulates the thinning regime, mode and intensity for different diameter classes. Hourly ecosystem carbon and water fluxes are calculated using meteorological forcing, which are integrated into daily, monthly and yearly time steps.

Drought-induced tree mortality is simulated by integrating detailed water balance calculations, physiological processes, and stress indicators. It captures the complex interactions between water availability, carbon dynamics, and tree physiology to predict tree responses to drought conditions, including the risk of mortality due to hydraulic failure or carbon starva-

tion (Nadal-Sala et al., 2017; Bugmann et al., 2019; Sperlich et al., 2020). Mortality functions related to hydraulic failure are tightly connected to the dynamics of water transport within the tree based on the idea of the Pipe model (Shinozaki, 1964) that describes a proportional link between leaf area and fine root biomass with the cross-sectional area of conducting sapwood. Mortality functions related to carbon starvation happens when prolonged drought reduces photosynthesis to the point where the tree cannot meet its metabolic demands of carbohydrates from the mobile C pool for maintenance, repair and growth. Additionally, the photosynthetic potential is coupled through a nonlinear relation to soil water content. The processes that lead to mortality are thus sensitive to both soil drought and meteorological drought. The model does not include other biotic/abiotic disturbances or extreme events (storm, fire, insect pests and diseases etc.) beside drought.

For this study, we used the pre-calibrated model from Sperlich et al. (2020) for Silver fir (*Abies alba* L.) which was parametrized and calibrated for the Black Forest in an interdisciplinary research project (BuTaKli, 2019).

LPJ-GUESS

LPJ-GUESS is a dynamic, process-based mechanistic vegetation model, which uses climatic and environmental input data to simulate terrestrial vegetation and soil dynamics at regional to global scale. In this study, we applied LPJ-GUESS version 4.1.2 (Hickler et al., 2012; Smith et al., 2014; Lindeskog et al., 2021) to simulate spruce monoculture forests in a specific grid cell in the Harz region. In LPJ-GUESS, the simulation of vegetation occurs within defined patches that correspond to fixed forest areas (0.1 ha in size). For forcing the LPJ-GUESS simulation we used daily climate data of ERA5 from 2000 to 2023. In this study, we used the ‘cohort’ mode of LPJ-GUESS. In this mode, vegetation is represented by cohorts, which are age classes within these patches. Within the cohort mode, each tree species cohort in a patch is represented by one average individual. Within each patch, cohorts of tree species and grass interact to establish, grow, compete for environmental resources and undergo mortality on a yearly basis. These dynamics are determined by species-specific parameters and the prevailing environmental conditions (Smith et al., 2001; Hickler et al., 2012; Smith et al., 2014).

Simulation settings: For our simulations, we followed the setup of Lindeskog et al. (2021) to simulate spruce monocultures. To build up soil, carbon, and nitrogen pools, we conducted a 1200-year spin-up period, which is considered standard for the LPJ-GUESS forestry version. The spin-up input data were based on the first 20 years of the historical ERA5 data. These data were internally detrended within the model, with the CO₂ concentration held constant throughout the spin-up period. Simulated species reflected the common European tree species initially parameterized by Hickler et al. (2012). CO₂ concentration data were taken from Meinshausen et al. (2011) and nitrogen deposition data from Lamarque et al. (2013). Soil properties were taken from Nachtergaele et al. (2009). Potential natural vegetation (PNV) stands were modelled using five replicate patches and the disturbance return interval was set to 400 years. From 1900 onward, PNV

stands were converted to planted spruce monoculture stands to simulate 110-year-old spruce stands. Spruce trees were planted according to land-cover data of Brus et al. (2012). This planted stand was modelled using a single patch, with fire mortality, stochastic disturbance events, thinning and harvesting all turned off. The conversion to monocultures was specified by input files in order to match age and species-composition in 2010. Norway spruce trees are planted with a tree density of 1,000 individuals per hectare.

S2: Initialization of forest model with artificial spruce forest data

The National Forest Inventory ('Bundeswaldinventur', BWI) employs a systematic sample inventory based on a 4 km × 4 km reference grid to document the forest conditions in Germany. To initialize the forest simulations, we selected a representative forest inventory from the 2012 BWI data set (<https://bwi.info/>; Riedel et al., 2017) that provides information on tree location, species and stem diameter. For our simulation experiment, we chose a site in the Harz Mountains that is an even-aged, old-growth spruce monoculture. The inventories have the size of a circle with a diameter of 20 metres. For the model simulations, however, a forest inventory of 1ha or 10ha is necessary, depending on the model. Therefore, the inventory data of the selected site was scaled to obtain a complete 1 ha and 10 ha initialization file by copying the original inventory data the appropriate number of times. In addition, tree age A was estimated from tree stem diameter D using the following regression term by analyzing the BWI dataset:

$$A = 24.7543 \times e^{0.02565 \times D \times 100}.$$

S3: Climate data

Copernicus ERA5-Land hourly data (Muñoz Sabater, 2019) for the period 2000–2023 has been obtained from the Copernicus Climate Change Service using the Climate Data Store (CDS) Python API. The data is provided in a regular latitude-longitude grid with a $0.1^\circ \times 0.1^\circ$ resolution. We have downloaded data for the grid cell containing the selected forest inventory location. Hourly data has been obtained for three variables: air temperature at 2 m above the surface, surface solar radiation downwards and total precipitation. The hourly values have been aggregated to daily values to yield the following input variables for the forest simulation models: (i) minimum, mean and maximum daily temperature ($^\circ\text{C}$), (ii) daily precipitation sum (mm) and (iii) irradiance ($\mu\text{mol} \times \text{m}^{-2} \times \text{s}^{-1}$).

S4: Estimating tree mortality from national crown condition survey

As reference mortality data the Germany-wide maps from Knapp et al. (2024) were used (available from: <https://doi.org/10.5281/zenodo.10805412>). These maps had been created following a statistical regionalization approach to obtain Germany-wide maps of annual mortality from the point samples of the crown condition survey (Knapp et al., 2024). For the reference time series in this study, spatial subsets of the

Harz ecoregion were taken from the spruce mortality maps and pixel values were aggregated to obtain the mean annual mortality rate in the region.

To produce the maps Knapp et al. (2024) used all live and dead trees from all crown condition surveys between 1998 and 2022 and combined them with a wide range of environmental predictor variables from the domains of climate, topography, soil, deposition and land cover. Logistic regression was used to identify the most important predictors and to model the probability of death for spruce under different conditions. The most important predictor variable for spruce mortality was the climatic water balance of the driest summer in the previous five years, i.e. drought and its legacy effect clearly turned out as the main driver. The regression model was then applied to predict the mortality rate for every hectare of spruce forest in Germany for each of the past 25 years.

S5: The drought index SPEI

The SPEI stands for the 'Standardized Precipitation Evapotranspiration Index'. It is a climate index designed to quantify the severity of droughts and wet conditions over time by combining both precipitation and potential evapotranspiration (PET), which is an estimate of the amount of water that would evaporate and transpire if sufficient water were available. The SPEI is standardized by comparing the observed data with a long-term record of similar values, resulting in a z-score-like value. Negative values indicate drought conditions, while positive values suggest wetter conditions. Here, the annual SPEI was calculated for a 12-month time period. We used the climate data (see supplementary information S3) and the SPEI package in R for the calculation. PET was calculated using the Thornthwaite equation. The monthly water balance was calculated as the difference between precipitation and PET.

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