Projecting Forest Dynamics Across Europe: Potentials and Pitfalls of Empirical Mortality Algorithms

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- Projections of forest ecosystem dynamics depend strongly on mortality algorithms
- Structure of empirical mortality algorithms is more important than geographic origin
- Including tree growth as indicator improved mortality predictions at multiple scales

MODEL AND DATA ARCHIVING:

Dynamic vegetation model ForClim available on the ETH Zurich server: https://uwis-server102.ethz.ch/openaccess/software/view/1

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T.T. and H.B. designed the study, T.T. conducted the simulation experiments and data analysis, T.T., L.H., M.C. and H.B. wrote the paper.

ABSTRACT

Mortality is a key process of forest ecosystem dynamics and functioning strongly altering biomass stocks and carbon residence times. Dynamic vegetation models (DVMs) used to predict forest dynamics are typically based on simple, largely data-free ('theoretical') mortality algorithms (MAs). To improve DVM projections, the use of empirically-based MAs has been suggested, but little is known about their impact on DVM behavior.

A systematic comparison of eight MAs (seven inventory-based, one 'theoretical') for the pan-European tree species *Pinus sylvestris* L. was carried out within the DVM ForClim for present and future climate scenarios at three contrasting sites across Europe. Model accuracy was furthermore evaluated with empirical data from young and old-growth forests.

We found strongly diverging mortality patterns among the MAs for present climate. Based on their behavior, we identified two distinct empirical MA groups that were related to their structure (i.e., variables considered), but not to their geographic origin (i.e., the environmental conditions they were calibrated to). Under climate change, MAs based on a competition index produced ecologically inconsistent results, while MAs based on growth showed more plausible and less extreme behaviors. Furthermore, MAs based on growth reached a higher accuracy for projecting young and old-growth forest dynamics.

Our results demonstrate that using empirical MAs in DVMs has a high potential to better predict forest dynamics, but also a risk of yielding implausible results if their structure is inadequate. For DVM applications across large spatiotemporal scales, we thus suggest using MAs based on growth, particularly under future no-analogue climates.

INTRODUCTION

The dynamics and functioning of forest ecosystems are inherently driven by demographic processes (Fisher et al., 2018), in particular tree mortality, which shapes forest structure, biomass and resource availability (Franklin et al., 1987). Consequently, much research has focused on better understanding the processes of mortality and its ecological consequences (Keane et al., 2001; Lutz and Halpern, 2006). A particular challenge lies in the multifaceted nature of mortality, which is caused by various processes that act on a continuum from the individual level (dominated by competition for resources) to larger scales (where disturbance-impacts predominate, e.g. windthrow and fire, Seidl et al., 2017; Thom et al., 2017). While significant progress has been achieved for disentangling drivers of disturbance-related mortality at the landscape scale (e.g., Temperli et al., 2015; Scheller et al., 2018), a high uncertainty remains for individual-scale mortality (Keane et al., 2001; Das et al., 2016). This type of mortality typically comprises stress-related processes (such as competition and unfavorable environmental conditions, e.g. drought, Bigler et al., 2006) and further causes of tree death (e.g., lightning strikes, mechanical breakage, etc., typically referred to as 'background mortality', Das et al., 2016). The uncertainty in individual-scale mortality has far-reaching consequences and can scale up to large variations in long-term projections of ecosystem dynamics and functioning (Friend et al., 2014; Bugmann et al., 2019).

Dynamic vegetation models (DVMs) have become an increasingly important tool for upscaling individual processes and projecting future forest dynamics (Shugart et al., 2018). However, individual-level mortality still remains poorly represented in DVMs, many of which rely on simplistic theoretical assumptions (e.g., Galbraith et al., 2010), or still use the same algorithm structure defined in the first generation of DVMs (Bugmann, 2001; Keane et al., 2001; Bircher et al., 2015). This slow pace of progress can be explained by the complexity of physiological mechanisms and the interwoven nature of multiple processes involved (Hartmann et al., 2018) as well as difficulties in empirically studying the rare and episodic process of mortality (Keane et al., 2001; Weiskittel et al., 2011). While simple, 'theoretical' mortality algorithms (MAs) lack a strong empirical basis (Wunder et al., 2008), 'physiologically-based' MAs require detailed process-level data and are currently not applicable to a larger number of species and mortality sources (McDowell et al., 2013; Hartmann et al., 2018). In the last years, an increasing number of studies have thus emphasized the benefits of using more empirically-based MAs that maintain a simple and generic structure, but are based on correlative relationships derived from large datasets (Adams et al., 2013; Hülsmann et al., 2018; Vanoni et al., 2019). By synthesizing empirical mortality patterns encoded in large-scale datasets (e.g. national forest inventories,

tree ring databases), empirical MAs may thus provide a potentially promising approach for a more accurate representation of mortality in DVMs (Adams et al., 2013; Cailleret et al., 2017).

Empirically-based MAs developed from forest inventories have a particular potential for the application in DVMs, as they are based on datasets covering large environmental gradients and a large number of species, thus facilitating their widespread application (Hülsmann et al., 2017). However, a primary source of uncertainty of this approach lies in the extrapolation of the MAs beyond their calibration range, i.e., the range of conditions represented in the underlying data (Adams et al., 2013). This effect is a key challenge in many ecological models (Yates et al., 2018) and is particularly relevant when applying empirical MAs outside their geographic origin (i.e., the environmental conditions they were calibrated to). Furthermore, biased tree size ranges in the calibration datasets can lead to extrapolation errors (Bircher et al., 2015). A good performance of MAs validated with empirical datasets under similar conditions (but outside of a DVM framework, e.g., Hülsmann et al., 2017) may thus not necessarily imply good performance for long-term projections within a DVM. However, very few studies have analyzed the implications of using empirical MAs within a DVM framework (e.g., Wyckoff and Clark, 2002), and little is known about their generality and limitations.

This lack of knowledge is particularly crucial in view of climate change impacts: higher temperature and altered precipitation patterns may create 'no-analogue' conditions (Williams and Jackson, 2007) where MAs can become less robust or even implausible (Keane et al., 2001). The response of empirical MAs to climate change also depends on their structure, i.e. their predictor variables, and their parameter estimates (Keane et al., 2001). Most empirical MAs for individual-level mortality (i.e., unrelated to large-scale disturbances) are based on tree size (diameter at breast height, DBH), since high mortality is characteristic of small trees (Hawkes, 2000) as well as tall trees, which are more vulnerable e.g. to hydraulic stress (Bennett et al., 2015). Empirical MAs differ, however, in the way they consider environmental effects and competition (e.g., via growth or a competition index, Weiskittel et al., 2011). Consequently, not only geographic origin, but also MA structure needs to be considered, particularly under 'no-analogue' climate conditions.

The objective of the present study was to address these knowledge gaps by a systematic evaluation of multiple empirical MAs within a consistent DVM framework (ForClim; Bugmann, 1996) and to explore their effects on simulated forest development across a large environmental gradient. The study focuses on MAs developed for the species *Pinus sylvestris*

L., which has a pan-European distribution (Mátyás et al., 2004) and thus allows for a cross-European comparison. In particular, we addressed the following research questions:

(1) How similar are mortality dynamics under present climate when simulated with the DVM ForClim in combination with different MAs? In particular, can clusters of MAs with similar behavior be associated with their geographic origin, MA structure, or other factors?

(2) How sensitive are simulation results with different MAs to climate change?

(3) How accurate are the DVM results with different MAs when confronted with independent empirical datasets for young and old-growth forests?

MATERIAL AND METHODS

Model ForClim

ForClim is a process-based DVM that simulates short- and long-term forest dynamics as an emergent property of environmental conditions and vegetation interactions (Bugmann, 1996). In this framework, a forest stand is divided into small patches (here 800 m², i.e. the size of a canopy gap created by the death of one large tree), where the life-cycle of tree cohorts (groups of trees of the same species and age) is simulated at an annual resolution. Tree demographic processes, i.e. establishment, growth and mortality, are simulated for each cohort and driven by environmental conditions (i.e., temperature, light, water and nutrients).

Overall, the model has been widely applied throughout Europe (e.g., Bugmann, 1996; Huber et al., 2018) and other parts of the temperate zone, including North America and Asia (e.g., Shao et al., 2001; Gutierrez et al., 2016). For the present study, the most recent version of ForClim (v4.0.1) featuring an improved representation of establishment, growth and mortality (Huber et al., subm.) was used (see Appendix A1 for details about ForClim). All simulations for this study were also carried out with an earlier, much different version of ForClim (v3.3, used by Mina et al., 2017), which yielded the same qualitative patterns and thus supports the robustness of our results to variations in DVM structure.

Mortality Algorithms

We compared seven inventory-based MAs developed for *Pinus sylvestris* by Monserud and Sterba (1999), Eid and Tuhus (2001), Palahi et al. (2003), Trasobares et al. (2004), Bravo-Oviedo et al. (2006), Crecente-Campo et al. (2010) and Hülsmann et al. (2018). These MAs were calibrated using data from National Forest Inventories (NFI), Permanent Sample Plots (PSP) or Natural Forest Reserves (NFR) (see Table 1). Geographically, they cover a cross-European gradient ranging from Mediterranean to temperate and boreal forests (Fig. 1). Methodologically, all MAs are based on logistic regression models (Monserud, 1976; Weiskittel et al., 2011), in which mortality probability ($p_{\Delta t}$) of tree i is expressed as:

$$p_{i,\,\Delta t} = \text{logit}^{-1}\,(X_i\,\beta) = \exp(X_i\,\beta)\,/\,(1 + \exp(X_i\,\beta)) \tag{Eq. 1}$$

with X_i denoting the design matrix of the linear predictor and β the respective parameter vector. In terms of algorithm structure, the MAs feature different predictor variables (Table 1). Most MAs use tree size (typically DBH) and competition (typically basal area of larger trees, BAL) as the main variables, with some models considering site index as indicator of its productivity.

Only two empirical MAs used growth as a predictor. A detailed description of the MAs including their predictor variables and their calculation in ForClim is given in Appendix A1. Since many DVMs incorporate a similar 'theoretical' representation of mortality (Keane et al., 2001), the 'theoretical' MA currently used in ForClim v4.0.1 was included for comparability. This MA comprises two components: (1) a species-specific 'background' mortality rate representing various mortality agents a tree is exposed to during its life (e.g., fungal infections, mechanical damage) based on the approach of Manusch et al. (2012), which incorporates a relationship between size and mortality. (2) A 'stress-induced' mortality component that represents increased mortality during times of slow growth (Bugmann, 2001). Details for the 'theoretical' MA are provided in Appendix A1.

Simulation approach

The simulations were carried out in three sets: Set 1 aimed at a systematic evaluation of the different MAs in ForClim under present and future climate conditions; Set 2 and Set 3 aimed at testing model accuracy for young and old-growth forest dynamics, respectively. Since the focus of this study was on mortality unrelated to disturbances, simulations for all three sets were carried out in the absence of management and other exogenous disturbances such as wind-throws, wildfires, or insect outbreaks.

Set 1: Systematic evaluation of mortality algorithms

For a systematic and comprehensive evaluation of the MAs within ForClim, a full factorial design was used. This allowed for testing the behavior of the MAs under a wide range of combinations of environment, competition, and tree sizes under clearly defined boundary conditions. Simulations were initialized with a pre-defined (planted) cohort of 250 trees of *Pinus sylvestris* (in the following referred to as the 'target cohort'), which represents a cohort of sufficiently large size to trace tree mortality over a simulation time of 1000 years. The simulations were carried out for three specific tree sizes (i.e., DBH at beginning of the simulation), referred to as 'Small' (DBH of 5 cm), 'Intermediate' (DBH of 20 cm) and 'Large' (DBH of 40 cm). This setup was chosen to explore the range of tree sizes that are underlying the empirical MAs (Table 1). To investigate the effect of competition on the mortality of the 'target cohort', taller cohorts of *Pinus sylvestris* were included as competitors in the simulation. They were initialized to produce a basal area of larger trees (BAL) of 10, 20, 30, 40 and 50 m^2 ha^{-1}, corresponding to the BAL range found in many calibration datasets (Hülsmann et al., 2017). It was furthermore assumed that these larger 'competing' cohorts were able to grow but

were not subject to mortality. These assumptions were necessary to avoid the confounding effects that (1) the 'target cohort' overgrew the competing cohort, and (2) higher mortality in the 'competing cohort' creates better growing conditions for the 'target cohort', thus leading to uncontrollable release effects at some point during the simulation. The simulations were carried out at three locations in Northern Europe (Jönköping, Sweden, temperature-limited conditions), Central Europe (Bern, Switzerland, optimum conditions) and Southern Europe (Léon, Spain, drought-limited conditions; Fig. 1) to test model behavior across a gradient of environmental conditions corresponding to their geographic origins (Table 1). Four climate scenarios were employed for this simulation set: one under current climatic conditions, and three assuming climate change scenarios with: (1) an increase in temperature by +4 °C ('*warmer*' scenario), (2) an increase in both temperature and precipitation (+4 °C and +20%, respectively; '*warmer and moister*' scenario), and (3) a temperature increase by + 4 °C and precipitation decrease by - 20% ('*warmer and drier*' scenario). Details about site location, environmental conditions and climate change scenarios are given in Appendix A3.

Set 2: Accuracy of mortality in young forests

To evaluate the accuracy of mortality in young forest dynamics (i.e. short-term simulations, <150 years), results were compared to empirical self-thinning data from fully-stocked, unmanaged experimental plots by Pretzsch (2006). For this set, a *Pinus sylvestris* stand with a defined stem density (6460 indiv. ha^{-1}) and tree size (mean DBH of 6.6 cm) was initialized to mimic a typical young stand growing under intermediate site conditions (site index of 20; see Lembcke et al., 2000), and run for 150 years. Since the focus of this simulation experiment was merely on self-thinning, subsequent management or tree regeneration was not included. The simulations were carried out at the study site Coburg (see Huber et al., 2018), located close to the experimental *Pinus sylvestris* plots of Pretzsch (2006) in Northern Bavaria (Fig. 1). Further site details are given in Table S1 in Appendix A3.

Set 3: Accuracy of mortality in old-growth forests

For evaluating the accuracy of mortality under old-growth forest conditions, emerging stand structures from long-term simulations were compared to the empirical data from the Pfynwald forest reserve (Brang and Heiri, 2011). It is located in the dry inner-alpine valley of the Valais in Switzerland, and represents one of the few unmanaged *Pinus sylvestris* forests in Central Europe that can be viewed as being in a dynamic equilibrium (Leibundgut, 1993). Stand structure in the reserve plots follows a typical reverse J-shaped diameter distribution with

abundant regeneration below a canopy dominated by a few large trees (Brang and Heiri, 2011). The simulations were started from bare ground with a simulation time of 1000 years assuming natural regeneration, as done in many simulation studies (e.g., Manusch et al., 2012). Further site details are given in Table S1 in Appendix A3.

Analysis of simulation outputs

For characterizing the mortality projections of Set 1, a measure describing the intensity of mortality for each MA was applied, defined as the time when 50% of the initial target cohort had died ($MT_{50\%}$). To account for effects of changes in competition (BAL) or with changing climatic conditions, a second measure ($\Delta MT_{50\%}$) was applied. $\Delta MT_{50\%}$ is defined as the change in $MT_{50\%}$ due to a change in BAL or climate ($MT_{50\%,i}$) relative to a baseline ($MT_{50\%,b}$):

$$\Delta MT_{50\%} = (MT_{50\%,b} - MT_{50\%,i}) / MT_{50\%,b} \qquad \text{(Eq. 2)}$$

Positive values of $\Delta MT_{50\%}$ thus indicate a higher mortality relative to baseline conditions (note that higher mortality leads to a lower value of $MT_{50\%}$ as a result of shorter tree lifespans). Baseline conditions were defined as the respective lower competition scenario (for analysis of response to competition) and as the present climate scenario (for analysis of response to climate change).

For evaluating the accuracy of mortality in Set 2, simulated self-thinning was expressed as logarithmic stand density (tree number per ha) versus mean tree biomass and compared to the corresponding dataset by Pretzsch (2006). For the evaluation of Set 3, mean basal area and stem density at the end of the simulation were compared to the range of both variables reported in all permanent plots of the forest reserve by Brang and Heiri (2011).

RESULTS

Set 1: Comparison of MAs under present climate

Simulated mortality dynamics showed high variability among the eight MAs (Fig. 2 and Fig. A4.1, A4.2 in Appendix). The differences were most pronounced for the 'large' trees (DBH = 40 cm) and in the absence of larger competing trees (BAL = 0). Under these conditions, several MAs projected exceedingly high survival rates with individual trees reaching ages of > 500 years. Increasing competition (i.e., higher values of BAL) increased the similarity of the mortality projections because all MAs predicted high mortality rates irrespective of their structure and parameter estimates. Notably, low-competition conditions resulted in faster growth, which led to an earlier exceedance of the DBH calibration range and thus an extrapolation of most MAs (indicated by dashed lines in Fig. 2).

The specific analysis of mortality intensity (defined as $MT_{50\%}$, i.e. the time when 50% of a cohort had died) and its sensitivity to competition ($\Delta MT_{50\%}$) also showed a clear differentiation among the eight MAs (Fig. 3). The different MAs followed an order of increasing $MT_{50\%}$ and sensitivity to competition (Fig.3a, direction bottom-left to top-right), starting from the 'theoretical' MA1 followed by MA2, 3, with the other MAs (4-8) reaching highest values. Increasing BAL resulted in smaller differences but generally the same patterns between the MAs (Fig.3b). Notably, the 'theoretical' MA showed a negative response to altered competition from BAL 0 to BAL 10 (Fig.3a), i.e. a minor increase in competition in this range decreased mortality probability. Initial tree size had a consistent effect on mortality intensity ($MT_{50\%}$) and competition responses ($\Delta MT_{50\%}$) among the different MAs. While competition effects were highest for the 'small' cohort size, the effect decreased with increasing tree size. Increasing tree size also led to higher $MT_{50\%}$ (i.e., lower mortality intensity), with the exception of MA3. Mortality patterns among the three sites were heterogeneous, showing opposite rank orders in mortality intensity ($MT_{50\%}$) from Leon to Jönköping to Bern between two MA groups, i.e. increasing $MT_{50\%}$ for the MAs 2 and 3, but reverse order for MAs 5,6,7.

Based on the overall mortality patterns (Fig.3) and the MA characteristics (Table 1) two groups were identified: MAs including a growth component ('Growth-based' MAs, i.e. the 'theoretical' MA1, as well as MAs 2 and 3) on the one hand, and MAs describing competition via a competition index ('CI-based' MAs, i.e. MAs 4-8) on the other hand. A higher similarity of MAs with a similar geographic origin (see Table 1) was however not evident (Fig. 3).

Set 1: Comparison of MAs under future climate

The changes of mortality intensity in the 'warmer' scenario (+4 °C) were relatively small across the sites ($\Delta MT_{50\%}$ range from -0.12 to + 0.15), but a clearer differentiation emerged for the 'warmer and moister' (+4 °C, +20% precip.; $\Delta MT_{50\%}$ range from -0.21 to + 0.30) and 'warmer and drier' (+4 °C, -20% precip.; $\Delta MT_{50\%}$ range from -0.51 to + 0.13) scenarios (Fig. 4). The direction of the response to climate change was generally consistent across the MA groups identified in the previous section and across sites (with the exception of Jönköping under the 'warmer' scenario, where most MAs predicted less mortality). The highest magnitude of change occurred at Leon, while only minor changes occurred for Jönköping and Bern except under the 'warmer and drier' scenario (Fig. 4). The 'CI-based' MAs (4-8) featured mostly a counter-intuitive pattern of higher mortality under a 'warmer and moister' scenario, but lower mortality under a 'warmer and drier' scenario. The 'Growth-based' MAs (1-3) showed the opposite response, i.e. they projected less mortality under the 'warmer and moister' but increasing mortality under the 'warmer and drier' climatic conditions (Fig. 4). In contrast to the sign of the response, the MAs showed little agreement regarding the magnitude of change (Fig. 4).

Set 2: Accuracy of mortality in young forests

In the self-thinning simulation experiment for young forests (age <150 years), the simulated relationships between stem density and biomass showed distinct differences among the MAs as well as to those reported by Pretzsch (2006) for unmanaged *Pinus sylvestris* stands (Fig. 5). While the 'theoretical' MA (1) as well as the MAs 2 and 8 were within the range of the observed data, the other MAs tended to underestimate mortality for all tree sizes (Fig. 5).

Set 3: Accuracy of mortality for old-growth forests

The long-term simulations at Pfynwald showed substantial differences in projected stand structure according to the MA that was used (Fig. 6), with 'Growth-based' MAs (1-3) producing more accurate results than 'CI-based' MAs (4-8). 'Growth-based' MAs predicted stand basal areas and stem densities that were close to reality, although some of these MAs tended to overestimate basal area and underestimate stem density (Fig. 6a,b). They also reproduced the pattern of abundant regeneration below a canopy dominated by a few, large trees (Fig. 6c1-3) as reported by Brang and Heiri (2011). In contrast, the 'CI-based' MAs consistently overestimated basal area and underestimated stem density (Fig. 6a,b). This was due to a simulated stand structure dominated by exceedingly large trees (>60 cm DBH) with practically no regeneration or mid-storey (Fig. 6c4-8), which was in stark contrast to observed stand structure (Fig. 6c9).

DISCUSSION

We found strong differences in DVM projections caused by the eight investigated MAs, which were largely associated with MA structure (particularly differentiating 'Competition index (CI)-based' and 'Growth-based' MAs), but not with their geographical origin. Below, we discuss these findings as well their implications for projecting the dynamics and functioning of forest ecosystems at large spatio-temporal scales.

General evaluation of MA behavior

Previous studies that investigated empirical MAs outside a DVM framework (e.g., Hülsmann et al., 2017) demonstrated the importance of the properties of the calibration dataset (geographic origin, DBH range, etc.). Given the wide geographical and environmental range covered by the MAs in our study (Table 1), we expected a strong influence of the MA's geographical origin, reflecting the different climatic drivers prevailing in the calibration range (e.g., low temperatures in boreal forests or drought in Mediterranean forests, see Kullman, 1997; Galiano et al., 2012, respectively). However, our study showed that within a DVM framework,

geographic origin was surprisingly unimportant compared to MA structure. This behavior was largely due to the representation of the direct and indirect effects of competition and the environment.

The 'CI-based' MAs incorporate variables that are directly associated with stand structure and competition (e.g., BAL, stem density, Eid and Tuhus, 2001; Crecente-Campo et al., 2010). In the simulations, better environmental conditions led to higher diameter growth, which in turn increased BAL. Consequently, trees experienced more competition and a higher mortality probability under better site conditions (favorable temperature and water availability) than under unfavorable conditions (e.g., Sterba, 1995; Monserud and Sterba, 1999). Most 'CI-based' MAs furthermore take into account environmental effects indirectly via a site index (see also Appendix A2). Instead of a site-specific representation of important environmental mortality sources (e.g., impacts of frost, heat or drought, Allen et al., 2010; Vanoni et al., 2016), site index typically accounts for higher mortality under better site conditions due to stronger competition and faster turnover (Weiskittel et al., 2011). While this approach is appropriate for applied questions of forest management under present climate, as shown in a number of studies (e.g., Eid and Tuhus, 2001; Bravo-Oviedo et al., 2006), our results demonstrate that it becomes problematic in global-change applications at larger scales. The lack of a variable accounting for the direct effect of harsh environmental conditions on mortality leads to a relatively low sensitivity of the 'CI-based' MAs to geographic origin. Moreover, the strong emphasis on competition (with unfavorable environmental conditions leading to a decrease in competition) causes the counter-intuitive pattern of a lower mortality intensity for sites with harsher environmental conditions (cf. Jönköping), which is at odds with large-scale patterns of forest mortality due to climatic stress (Allen et al., 2010; Thurner et al., 2016; Greenwood et al., 2017).

In contrast, 'Growth-based' MAs (1-3) assume that slow growth leads to increased mortality probability, as frequently observed in dendroecological studies (e.g., Bigler and Bugmann, 2004; Cailleret et al., 2017). This relationship leads to an increasing mortality under high levels of competition, which is typically observed in small size classes (Hawkes, 2000), particularly during the early stages of forest development (e.g., Lutz and Halpern, 2006). With respect to unfavorable environmental conditions, this group of MAs responds with an increasing mortality probability (as reported e.g. for trees impacted by drought or frost, Vanoni et al., 2016). The focus on growth as an indicator for vitality integrates the effect of unfavorable environmental conditions (e.g., limitations by light, temperature, water) on decreased photosynthesis, changes in carbon allocation patterns and ultimately decreased survival probability (Dobbertin, 2005;

Wunder et al., 2008). Our results show a higher intensity of mortality at sites characterized by strong drought and temperature limitations (i.e., Jönköping and Léon) for the 'Growth-based' MAs, which is in line with both fundamental principles of stress mortality (Franklin et al., 1987; Niinemets, 2010) as well as patterns of climate-related mortality reported at larger scales (Thurner et al., 2017).

Among the 'Growth-based' MAs, the 'theoretical' MA of ForClim showed a unique behavior featuring a lower mortality probability with a small increase in competition (cf. Fig.3), which allowed trees to reach older ages. Noticeably, the 'theoretical' MA takes into account maximum size, following the approach of Manusch et al. (2012) (see Appendix A1 for details). This design leads to two counteracting mechanisms: at lowest competition (BAL 0), trees reach their maximum size faster, which decreases their life expectancy. A minor increase of competition (BAL 10), however, reduces growth moderately, which thus allows trees to reach higher longevity. At first sight, this behavior is counter-intuitive, but it is actually representing the trade-off between early growth rate and lifespan that has been observed across multiple tree taxa (Bigler and Veblen, 2009; Bigler, 2016).

Overall, we found that within a DVM framework, differences in MA structure (particularly the representation of competition *vs*. the environment) played a decisive role, with only MAs based on growth producing ecologically plausible behavior across a wide environmental gradient.

Response of MAs to climate change

An adequate representation of mortality in DVMs is particularly important in the context of climate change projections (Keane et al., 2001), and can have far-reaching implications for global vegetation cover and the carbon cycle (Adams et al., 2013; Friend et al., 2014; Thurner et al., 2017). Previous studies have shown that DVM projections under climate change can vary drastically with alternative MA formulations (e.g., Bircher et al., 2015; Bugmann et al., 2019). The results from the present study extend these findings to a wide range of geographically and structurally different MAs and furthermore highlight that even opposite DVM responses to climate change can occur, depending on the type of MA structure. The two MA groups identified here under present climatic conditions exhibited similar behavior under climate change scenarios, which was due to the same underlying mechanisms (cf. preceding section). Under warmer and drier climatic conditions, the 'CI-based' MAs decreased the mortality rates due to the reduction of competition intensity. This behavior is in stark contrast to various empirical and modeling studies showing substantial increases in drought-related mortality with

ongoing climate change (Allen et al., 2010; Anderegg et al., 2013; Greenwood et al., 2017). The 'CI-based' MAs may thus be suitable for short-term applications under analog climatic conditions (e.g., Crecente-Campo et al., 2010), but they are likely to be structurally inadequate to represent climate change effects on mortality and thus may lead to unexpected and extreme behaviors in DVMs (cf. Williams and Jackson (2007) and Yates et al. (2018) for similar problems in other ecological models). The behavior of the 'Growth-based' MAs (relying on growth as a climate-sensitive indicator for tree vitality, Dobbertin, 2005) was in much better agreement with expected mortality responses under a warmer and drier climate (Allen et al., 2010; Allen et al., 2015). The results from our study thus suggest that 'Growth-based' MAs provide an ecologically consistent and more robust alternative for projecting climate change-related mortality in DVMs.

From a methodological point of view, it should be noted that MAs based on forest inventories or other data sources that do not feature an annual resolution tend to underestimate the effects of abrupt growth changes due to shorter-term environmental impacts and may fail to predict mortality induced by extreme events, especially for angiosperms (Cailleret et al., 2017). A potential solution to this problem may lie in an a fusion approach of inventory and tree-ring based MAs, as recently provided by Vanoni et al. (2019). The benefit of annual data for improving empirical MAs could be further increased if information on tree mortality causes at different size classes were recorded (e.g., Lutz and Halpern, 2006; Das et al., 2016). These datasets are of particular value, as they allow to disentangle the multifactorial nature of mortality and to identify climate-sensitive drivers (e.g., the role of insects, see Das et al., 2016).

Evaluation of MA accuracy

Evaluating DVM dynamics at different developmental stages (as in our case 'young' and 'old-growth' forests) is of key importance for assuring accurate projections of forest dynamics (Brazhnik and Shugart, 2016; Huber et al., 2018). Compared to empirical patterns for both developmental stages, the 'Growth-based' MAs (particularly MA 1 and 3) performed best, while the 'CI-based' MAs (4-8) were mostly outside the observed data range. A consistent result was the underestimation of mortality in the self-thinning stage (young forest simulations) and over-predictions of the abundance of large, old trees (old-growth simulations) for the 'CI-based' MAs, which led to a failure of reproducing a reverse J-shaped diameter distribution (Brang and Heiri, 2011). Most 'CI-based' MAs were developed for relatively short-term projections in a forest management context and were fitted to NFI or PSP data (Eid and Tuhus,

2001; Crecente-Campo et al., 2010). In these managed forests, large trees are strongly underrepresented, as trees are typically harvested at target diameters of ca. 40-60 cm (typical rotation periods for Pinus sylvestris <120 years, Holgen et al., 2000). As these biased dataset lack significant mortality of larger size classes (see Monserud and Sterba, 1999; Weiskittel et al., 2011), the extrapolation of 'CI-based' MAs in a DVM can lead to a situation where the largest, dominant trees have a very low mortality probability. This behavior can also be observed in Fig.2, where exceedingly high longevities (> 500 years) were projected (while empirical measurements only rarely report ages > 300 years for *Pinus sylvestris*, e.g. Mason et al., 2007). This problem has been noted in some studies developing 'CI-based' MAs, but is generally considered as unimportant for short-term applications in a management context (e.g., Trasobares et al., 2004). The 'Growth-based' MAs, in contrast, were developed with the objective of representing longer-term dynamics, and thus they included relatively long monitoring times (>30 years), and in the case of MA 2 (Hülsmann et al., 2018) focused on strict forest reserves. Although very large trees are underrepresented even in strict forest reserves in Central Europe (Hülsmann et al., 2018), the longer time scales of monitoring increase the probability of adequately characterizing infrequent, episodic mortality events (Lutz and Halpern, 2006). Altogether, the higher mortality rates led to a to a smaller number of large trees and a continuous regeneration at the forest floor for the 'Growth-based' MAs, which was consistent with the observations from old-growth *Pinus sylvestris* reserves in both the Pfynwald and Northern Europe (Brang and Heiri, 2011; Wood and Bunce, 2016).

Implications for projecting dynamics and functioning of forest ecosystems

Changes in forest structure are inextricably linked to altered ecosystem functioning (e.g., Rödig et al., 2018). This aspect is of particular importance, as DVMs play a key role for projecting future forest structure and functioning at large spatio-temporal scales (Thom et al., 2017; Shugart et al., 2018). Our results show that different MAs can lead to drastically different projections of forest structure, thus highlighting the relevance of carefully selecting appropriate empirical MAs at large scales.

With respect to spatial scales, DVMs are increasingly used in combination with remote sensing data to project carbon stocks and fluxes in forests at the regional to continental scale (e.g., Shuman et al., 2011; Rödig et al., 2018). Applying structurally inappropriate empirical MAs (i.e. insufficient representation of climate drivers) can cause severely erroneous DVM behaviors at this scale, with effects likely to increase towards regions where climate-related stress (e.g., water or temperature limitation) becomes pivotal (Boisvenue and Running, 2006;

Thurner et al., 2016). An MA underestimating climate-related mortality can thus lead to a strong overestimation of biomass and carbon stocks in these regions. Furthermore, effects on microclimate and hydrology may be underestimated, which are progressively explored with DVMs at large spatial scales as well (e.g., Yang et al., 2015; Thom et al., 2017).

With respect to temporal scales, our results show that the effects of MA choice increase with projection timespan and the magnitude of the climate change scenario applied. As shown for the underestimated mortality for large trees in the case of the 'CI-based' MAs, this can result in the long-term buildup of an excessive carbon stock and an overestimation of carbon residence time in terrestrial vegetation (see also Friend et al., 2014).

In conclusion, the use of empirical MAs in DVMs offers a high potential but requires particular caution regarding the choice of the MA structure. Our results suggest that MAs based on growth offer a suitable structure, especially for DVM applications to project forest dynamics and functioning at large spatio-temporal scales.

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TABLE LEGENDS:

Table 1: Mortality algorithms (MAs) and their type, geographic origin, calibration data (NFI: National Forest Inventory, PSP: Permanent Sample Plots, NFR: National Forest Reserves), observation period between the first and last inventories (Time), measured diameter ranges in the calibration dataset (DBH_{min} and DBH_{max} in cm), as well as their predictor variables (Size: diameter at breast height (DBH), Growth: radial tree growth, Density: number of trees per ha, Site index: height of dominant trees at a specific age). For further information about empirical MAs and their variables, see Appendix A2. Additional information about the calibration datasets are given in table A2.

TABLES

MA Type	MA-Nr	Study	Country/Region	Data Type	Time	DBH$_{min}$	DBH$_{max}$	Predictor variables				
								DBH	Growth	BAL	Density	Site index
Theoretical	1	Huber et al. (in prep)	-	-	-	-	-	x	x			
Empirical	2	Hülsmann et al. (2018)	Lower Saxony, Germany, and Switzerland	NFR	1961 - 2014	4	78	x	x			
Empirical	3	Palahi et al. (2003)	North-East Spain	PSP	1964 - 2000	5	55.6		x	x		
Empirical	4	Trasobares et al. (2004)	Catalonia, Spain	NFI, subset	1989 - 2001	7.5	76.4	x		x		
Empirical	5	Monserud and Sterba (1999)	Austria	NFI	1981 - 1990	5	(50)	x		x		
Empirical	6	Bravo-Oviedo et al. (2006)	Spain	PSP	1960-	4.1	69.1	x		x		x
Empirical	7	Eid and Tuhus (2001)	Norway	NFI	1986 - 1998	5	46.3	x		x		x
Empirical	8	Crecente-Campo et al. (2010)	Galicia, Spain	PSP	1996 - 2003	5	49.2	x		x	x	x

Figure 1: Geographic origin of empirical mortality algorithms (marks indicate the country or approximate region of origin) and locations of the study sites across Europe.

Figure 2: Simulated mortality dynamics by ForClim using eight MAs for the site Bern. Lines represent the development of tree mortality of the 'target cohort' (see section 'Simulation approach') over time for three initial sizes of the target cohort and six levels of competition. Initial tree sizes were 'Small' (DBH of 5 cm), 'Intermediate' (DBH of 20 cm) and 'Large' (40 cm). Competition was defined by basal area of larger trees (BAL in m^2 ha^{-1}). Dashed lines indicate that the MA exceeded its calibration range in terms of tree size (DBH). Note that the 'theoretical' MA has no DBH calibration range.

Figure 3: Comparison of model behavior based on the projected mortality intensity ($MT_{50\%}$) and the response to competition ($\Delta ML_{50\%}$, i.e. change in $MT_{50\%}$ for an increase of BAL by 10 m^2 ha^{-1} relative to baseline BAL) of eight alternative MAs for (a) BAL 0 and (b) BAL 10 as a baseline. Note that symbol size indicates initial tree size, symbol type indicates the study site, and symbol color indicates the different MAs. Note that cases with an $MT_{50\%} > 1000$ years (i.e. those that did not reach 50% of mortality during the entire simulation period) cannot be displayed.

Figure 4: Change of mortality intensity ($MT_{50\%}$) under future climate relative to present climate conditions (for BAL 10 and target cohort 'Medium' size) for the different MAs. Responses were similar for different target cohort initial sizes and BAL conditions, see Appendix A4 (Fig. A4.3-4.5).

Figure 5: Comparison of self-thinning projections (density and mean tree biomass) by the eight MAs implemented in ForClim for the site Coburg with empirically measured data by Pretzsch (2006) for six unmanaged, fully stocked *Pinus sylvestris* stands in Bavaria, Germany. For details about the calculation of tree biomass in ForClim, see Appendix A2.

Figure 6: Comparison of stand basal area (a), stem density (b), and DBH distribution (c) simulated by ForClim at the Swiss site Pfynwald (1000-years simulation) with measured data from Brang and Heiri (2011) (blue area indicating the range, blue line indicating median of measured data). Only trees >8cm DBH were included to allow for a comparison with the empirical data. Note that 'Measured range' (subfigure a,b) represents the range in all reserve plots, while subfigure c9 depicts a detailed stand structure measurement from the largest, undisturbed subplot ('Abteilung 3').
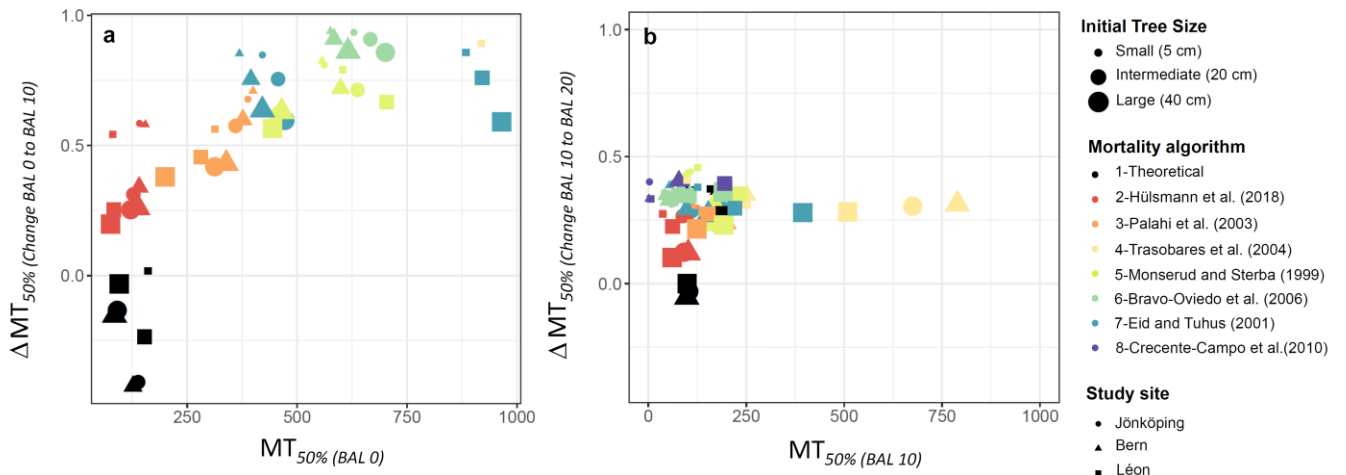
FIGURES
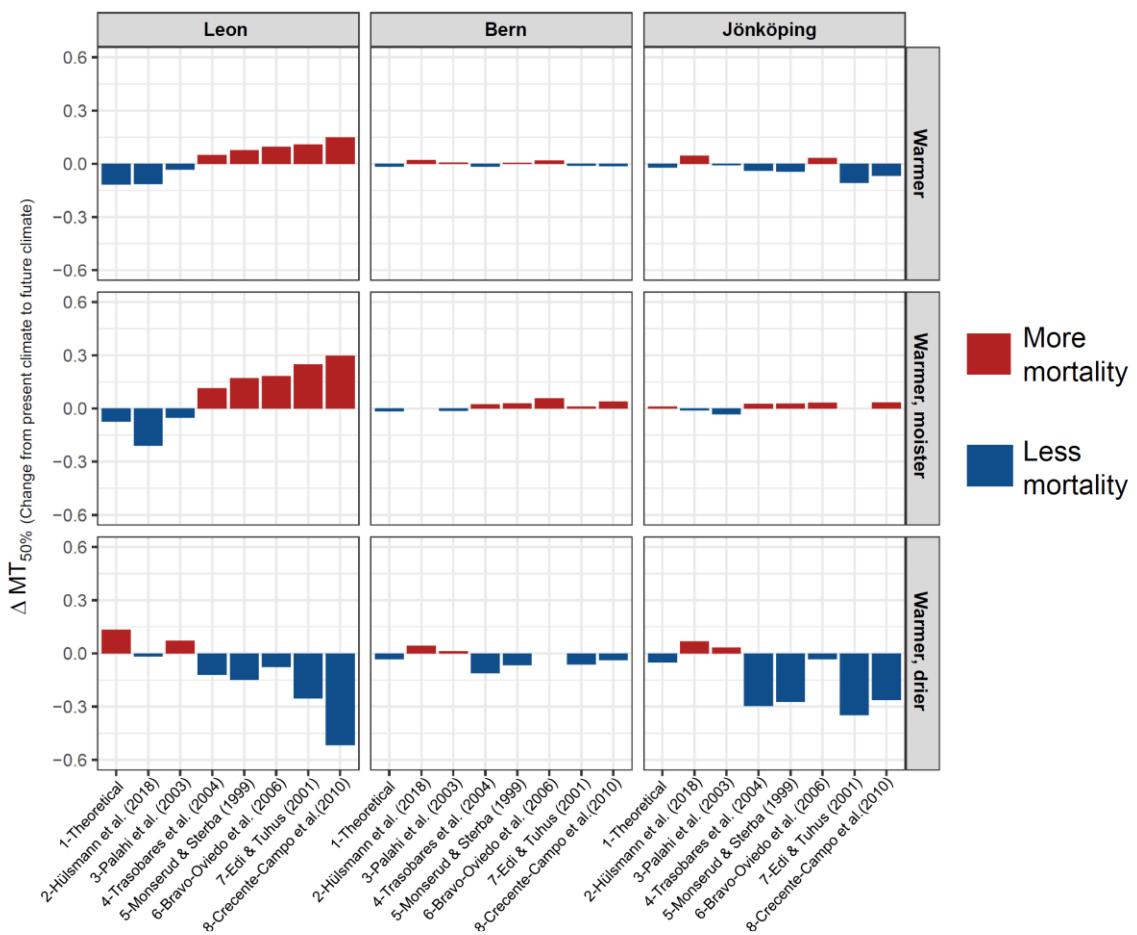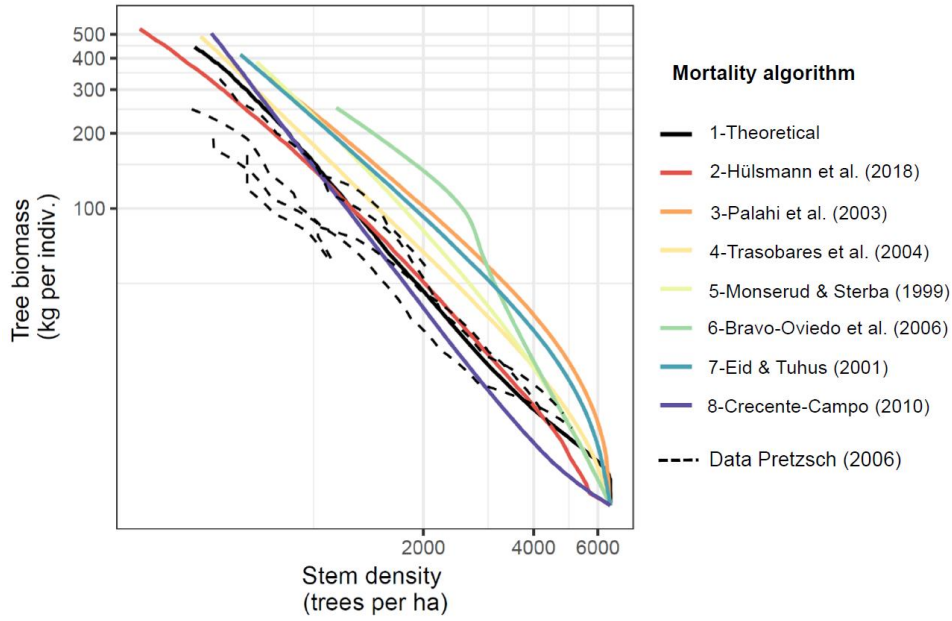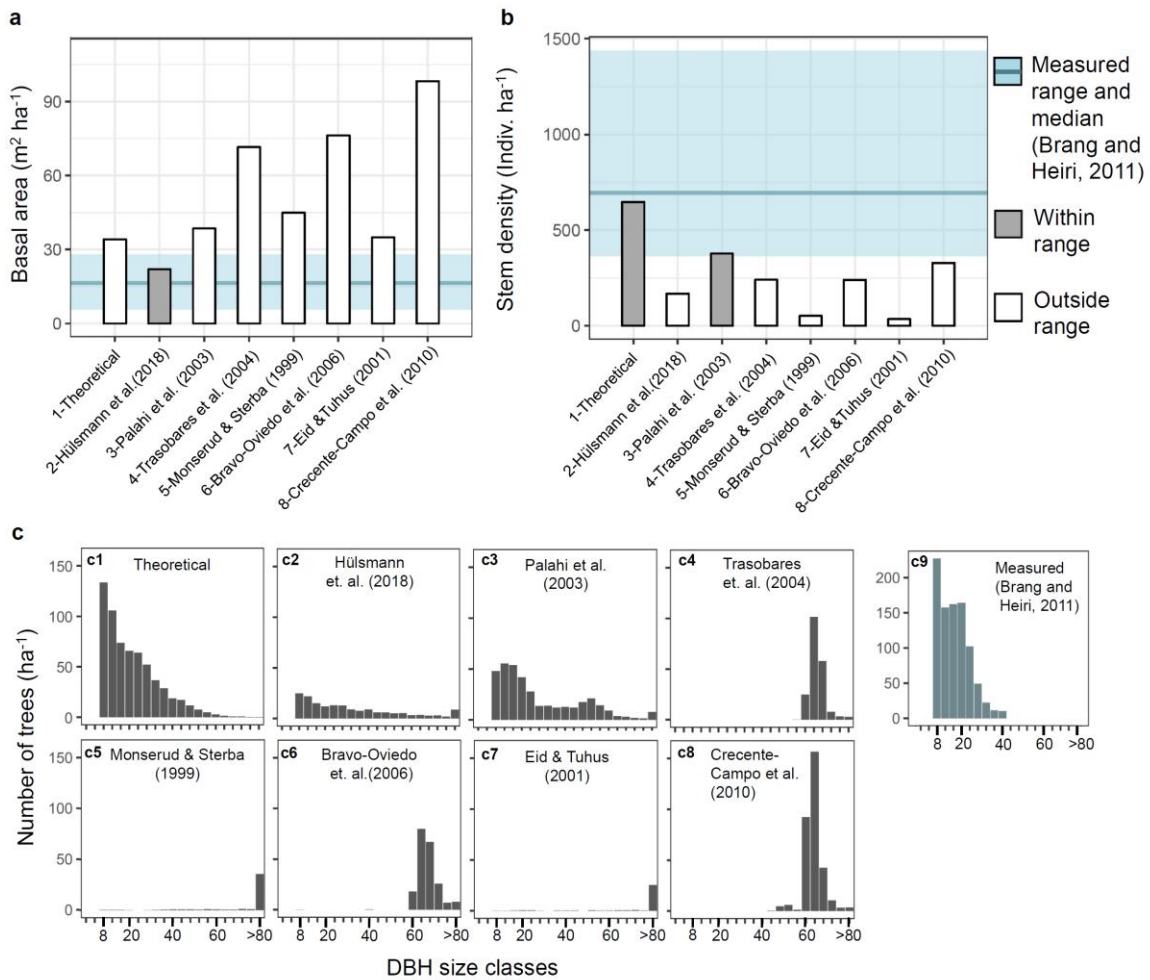

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Figure 1

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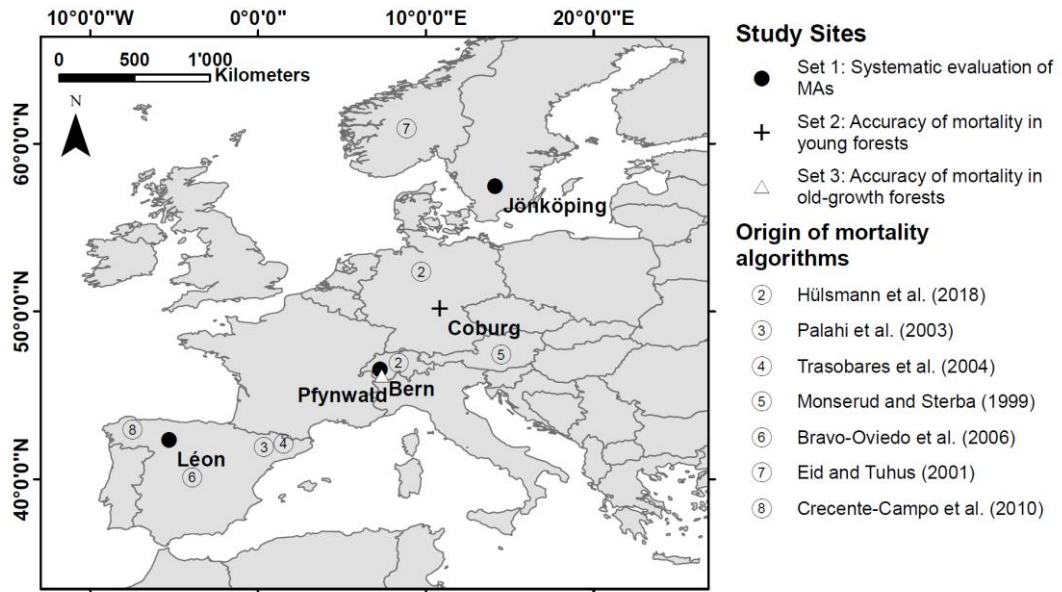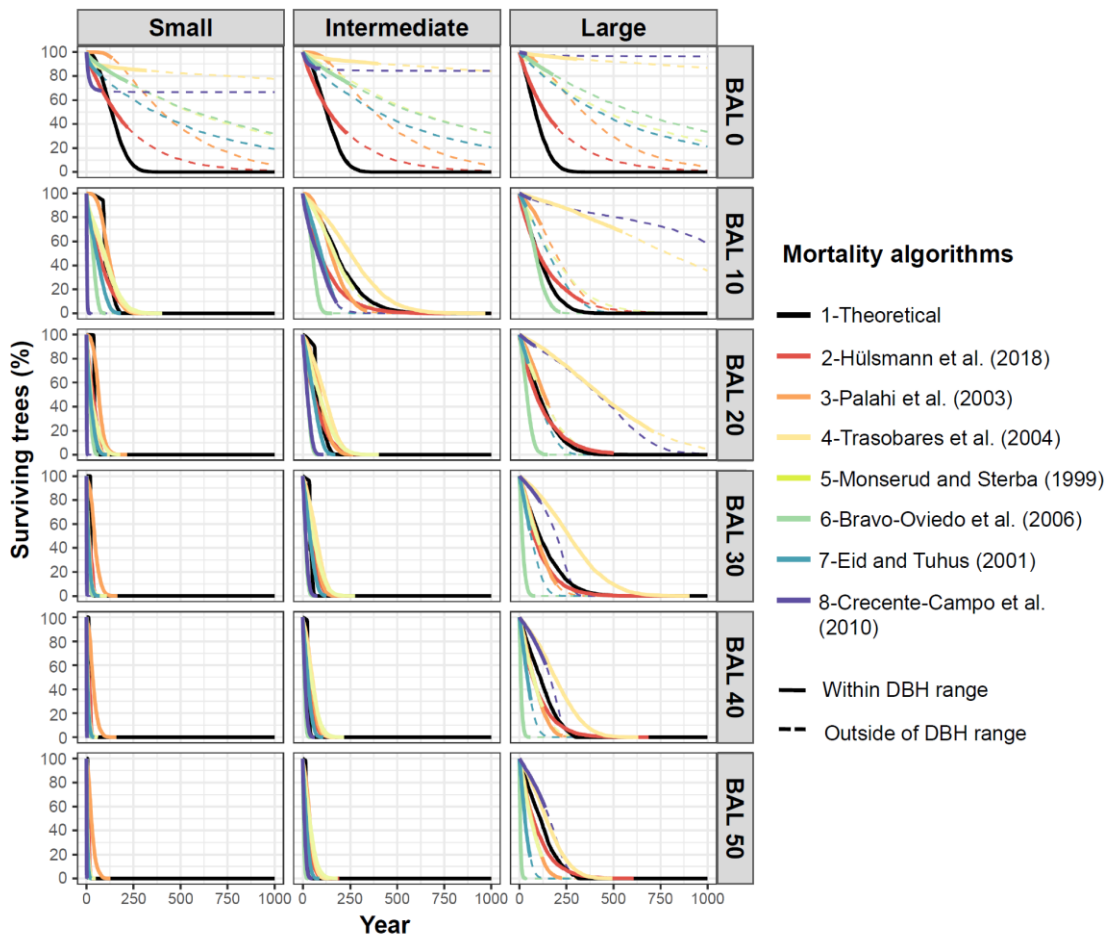
Figure 2

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