



Empirical and process-based approaches to climate-induced forest mortality models

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Globally, forests store ~45% of carbon sequestered terrestrially, contribute more to the terrestrial sink per area than any other land cover type, and assimilate an important portion of anthropogenic emissions (Bonan, 2008). Forests exert strong biophysical control on climate via surface energy balance (Bonan, 2008; Rotenberg and Yakir, 2010; Houspanossian et al., 2013), and the hydrological cycle (Zhang et al., 2001; Brown et al., 2005). Widespread forest mortality in response to drought, increased temperatures, and infestation of tree pests has been observed globally, potentially threatening forests' regulation of climate (Kurz et al., 2008; Adams et al., 2010; Allen et al., 2010; Anderegg et al., 2013a). This threat has prompted great interest in understanding and predicting tree mortality due to climate variability and change, especially drought. Initial tests of hydraulic failure (mortality caused by irreversible loss of xylem conductivity from air embolism), carbon starvation (mortality due to carbohydrate limitation), insect attacks, wildfire, and their interdependence (Allen, 2007; McDowell et al., 2008, 2011, 2013a), suggest proximal causes of mortality are likely complex, co-occurring, interrelated, and variable with tree species (supported by Adams et al., 2009, 2013; Sala et al., 2010; Piper, 2011; Zeppel et al., 2011; Anderegg et al., 2012a, 2013b; Adams et al., 2013; Anderegg and Anderegg, 2013; Galvez et al., 2013; Gaylord et al., 2013; Hartmann et al., 2013a,b; Mitchell et al., 2013; Quirk et al., 2013; Williams et al., in review). While the interdependent roles of carbon and water in plant mortality

are consistently observed, this work is continuously prompting new questions (Sala et al., 2010; McDowell et al., 2013b; O'Grady et al., 2013).

The justification for physiological research on drought-induced tree mortality is often stated as a need to improve the predictive capability of vegetation models through incorporation of mortality mechanisms (Fisher et al., 2010; McDowell et al., 2011, 2013a; Powell et al., 2013). Yet if mortality is particularly complicated and associated with failure of multiple physiological processes (Manion, 1981; McDowell et al., 2011; Anderegg et al., 2012b), then a key question emerges: is a mechanistic approach necessary for accurate prediction of future mortality? The answer to this question ultimately depends on the application and goal of the model.

At issue is whether increasing model complexity will improve prediction, which is influenced in part by the modeling approach employed. Two endpoints on a theoretical continuum of approach to mechanism are process-based and empirical model types. The process-based approach focuses on simulating detailed physical or biological processes that explicitly describe system behavior, while the empirical approach relies on correlative relationships in line with mechanistic understanding, but without fully describing system behaviors and interactions (Korzukhin et al., 1996; **Table 1**). Process-based models can be more comprehensive and incorporate mechanism explicitly, while the empirical approach is typically simpler, with mechanism implicit. These approaches are not exclusive model classifications;

All process-based models include some empirical information (e.g., in the choice of relevant mechanisms), and the correlative relationships of empirical models assume a link to process (Korzukhin et al., 1996; Makela et al., 2000). Realistically, many models use a hybrid approach, combining process-based and empirical representation of relationships.

The advantages and disadvantages of both approaches have been well acknowledged in ecology (Korzukhin et al., 1996; Levin et al., 1997; Makela et al., 2000; Green et al., 2005; Van Nes and Scheffer, 2005). Uncertainty in process-based model outputs could be higher than for the empirical approach due to greater model parameters and data inputs to represent the many processes in the system (**Table 1**). In the empirical approach, model uncertainty may be reduced, yet significant bias can result from exclusion of important system components by extrapolation of correlative relationships beyond observed variability. Process-based models can better include novel or no-analog responses, those which may occur with future conditions but are not well quantified in past observations (Williams and Jackson, 2007). Ensembles of multiple models are often implemented in climate prediction (Jones, 2013), and can be used to reduce uncertainty in biological responses to climate change (Asseng et al., 2013). An ensemble approach for forest mortality should include models from across the spectrum of empirical to process-based types (e.g., McDowell et al., 2013a). In previous decades, process-based modeling was often limited by computing power, but improvement is now frequently limited

Table 1 | Relative differences in the characteristics of process-based and empirical modeling approaches.

	Process-based	Empirical
Relationship type	Causal	Correlative
Relative comprehensiveness	More comprehensive	Less comprehensive
Incorporation of mechanism	Explicit	Implicit
Primary source of error	Unknown parameters and processes	Extrapolation
Model uncertainty	Higher	Lower
Data requirements	Higher	Lower
Spatial scale for calibration	Smaller	Smaller to larger
Spatial scaling of prediction	Smaller to Larger	Best at scale of calibration

by availability of data needed to initialize, parameterize, and evaluate models (Hall, 1988; Onstad, 1988; Levin et al., 1997; McDowell et al., 2011).

The decision between using relatively process-based or empirical approaches also depends on the scale of spatial and temporal inference. For example, to quantify the feedback of vegetation impacts upon future climate, reliable predictions of forest mortality at the global scale should be simulated. However, most field studies have focused on small scales. Therefore, techniques to extend small-scale understanding to large-scale models are critically needed (McDowell et al., 2013a). Models developed at the plot scale often have data input requirements that are not available at larger scales. This is a particularly important problem for more process-based models, which typically require more data inputs (Table 1). In contrast, because the mechanisms leading to mortality could differ among regions and species, relatively empirical models developed for one location/region or species may not be applicable to another, necessitating development for each region or species. Process-based models are more robust for scaling across regions and species due to the coupled representation of multiple basic processes; however, model simplification may be necessary in order to make the large-scale simulation feasible in respect to computational cost and data requirements.

Both process- and empirically-based models suffer from two large data-gaps. First, most mortality studies have focused on a few species, but for a global simulation, comprehensive representation of many species across different regions is

required. This has been achieved by grouping species into functional types (Woodward and Cramer, 1996), but future research should refine these groups based on empirically determined links between species drought strategies and mechanisms of mortality. Second, to evaluate models at different scales, it is important that we have comprehensive mortality benchmarking datasets across different regions and functional types. Currently, few such datasets are available, substantially limiting mortality model progress at large scales (Allen et al., 2010).

The challenge of bridging mechanism and scales is arguably greatest at the global scale, where finer scale processes (e.g., photosynthesis) must be simulated across the Earth. Dynamic global vegetation models (DGVMs) coupled with general circulation models are a common tool for simulating vegetation response to climate change (Sitch et al., 2008; Jiang et al., 2013). Early DGVMs that specifically included forest mortality represented mortality simply, with routines representing the stem exclusion phase (intra-species competition) of forest stand development and/or dependent on minimum productivity thresholds for tree survival (Bugmann, 2001; Cox, 2001; Sitch et al., 2003, 2008; see also Box 1 in McDowell et al., 2011). There has been increased effort toward representing forest mortality in DGVMs with more detail using process-based approaches. In a recent version of the Community Land Model with dynamic vegetation enabled (CLM4-CNDV), which is based on the Lund-Potsdam-Jena model (Sitch et al., 2003), vegetation represented by plant functional types is established and changes

according to biogeography rules based on temperature thresholds and a minimum precipitation requirement (Levis et al., 2004; Oleson et al., 2010). Annual mortality can occur in the model due to light, competition, fire, growth efficiency, and heat-stress tolerance (Levis et al., 2004; Jiang et al., 2013; Figure 1). The Ecosystem Demography model (Moorcroft et al., 2001) has been updated with algorithms for tree carbon resources and xylem cavitation to represent carbon starvation and hydraulic failure mechanisms (Fisher et al., 2010; McDowell et al., 2013a). Other process-based models not linked to DGVMs have been developed to predict tree mortality at stand to regional scales. These include TREES, which simulates mortality from gas exchange, soil-plant hydraulics, and carbohydrate dynamics (Lorant et al., 2010; Mackay et al., 2012; McDowell et al., 2013a), and LANDIS-II, a forest succession model extended to predict mortality from drought duration and intensity (Gustafson and Sturtevant, 2013). Epidemiological models that incorporate tree stress and insect population dynamics have also used a relatively process-based approach (Powell and Bentz, 2009).

In contrast to process-based approaches for tree mortality simulation, simpler, more empirical methods could offer valid and rapid alternatives for projection of climate change effects on forests. Manion's (1981) pre-disposing factor framework has been used to predict tree vigor decline that leads to death at the level of individual trees (Güneralp and Gertner, 2007) and vulnerability to insect attack at the stand level (Coops et al., 2009). Xylem resin anatomy, which integrates tree stress and defense against bark beetles, was an effective predictor of individual tree mortality (Kane and Kolb, 2010), and may be a productive avenue for model development using simple climate-xylem resin anatomy relationships from tree-rings. Bioclimatic envelope models are an example of a primarily empirical approach often used to predict tree species response to future climate (e.g., Iverson et al., 1998, 2008; Rehfeldt et al., 2012). In these models the relationship between the current climate at species' range limits are used to predict future distributions by moving these species' range limits

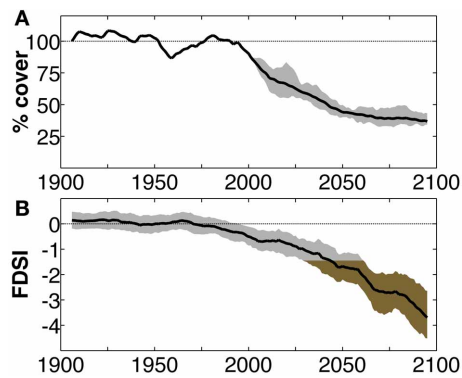


FIGURE 1 | A comparison of tree mortality projections for the southwest USA from a more process-based Dynamic Global Vegetation Model, and a less process-based, empirical index that could be applied in a mortality model. (A) Projected heat-induced decline in relative conifer forest cover using the Community Land Model with dynamic vegetation enabled (CLM4-CNDV; Jiang et al., 2013), with the ability to account for the impact of declining forest population on mortality rate. Shading bounds eight projections assuming unique model-projected scenarios of global sea surface temperatures. Black line: ensemble mean. **(B)** Forest Drought Severity Index (FDSI) predicted through 2100 by applying an empirical growth-climate relationship to modeled projections of precipitation and vapor-pressure deficit (Williams et al., 2013). More negative values indicate intensified forest stress. Shading bounds the inner quartiles of CMIP3 model projections. Brown shading represents FDSI values more severe than the estimated regional mortality threshold (-1.41 , average FDSI of the most severe 50% of years during the 1573–1587 megadrought). Black line: ensemble mean. Note the inflection point in the decline of forest cover in **(A)** corresponds with FDSI crossing the regional mortality threshold (2030–2060) in **(B)**. Both imply similar predictions for mortality, and each model incorporates information that the other could benefit from.

to match the location of these climate envelopes under future conditions (see **Table 1** in Araújo and Peterson, 2012). When appropriately used, this approach projects potential tree species habitat, not actual future distributions (Iverson et al., 2008; Araújo and Peterson, 2012), although similar relationships are used for survival thresholds in Lund-Potsdam-Jena and other DGVMs (Sitch et al., 2003; Jiang et al., 2013). Development of mortality-specific envelopes or empirical indices with climatic and environmental (e.g., soil moisture) thresholds for tree survival that have been directly tested or observed would improve predictions based on these relationships.

There can be different levels of complexity in such empirical approaches. For example, the forest drought stress index (FDSI), derived from tree-ring records and predictable from regional climate, is highly correlated with forest mortality in the southwest USA (Williams et al., 2013, **Figure 1**). Williams et al. infer FDSI through AD 2100 from climate projections and empirically predict that by mid-century the southwest USA will be less suitable for forests than in at least 1000 years due to increasing atmospheric mois-

ture demand. The timing of mortality implied by the FDSI projection coincides with the period of rapid forest loss predicted in recent simulations using the Community Land Model coupled with nitrogen and vegetation dynamics (CLM4-CNDV; Jiang et al., 2013). The CLM4-CNDV uses an empirical approach of mortality, including thresholds of growth rate and heat stress, and moisture limitations, but relies on explicit process simulation including photosynthetic simulation for vegetation growth (Jiang et al., 2013; **Figure 1**). The relationship between FDSI and recent tree mortality rates (see **Figure 2** in Williams et al., 2013) suggests a potentially simpler empirical application for this stress index in a mortality model. The FDSI approach requires development of empirical climate-tree stress and mortality relationships for a specific region, while the dynamic vegetation approach of Jiang et al. (2013) simulates universal forest interactions with climate. Although the DGVM is much more complex than the empirical relationships in an FDSI approach, results from both are similar for the southwest USA (**Figure 1**). Thus, the empirical approaches like FDSI are simple but powerful, and regionally based

empirical results may inform DGVMs regarding climatic threshold effects on vegetation.

With an imperfect understanding of the physiological processes involved, we currently cannot discern the causes of tree mortality from the symptoms of dying. For example, it is not known whether the carbohydrate depletion observed as some trees die from drought may be a resultant symptom of mortality by hydraulic failure, or a directly contributing cause of mortality (McDowell et al., 2011; Adams et al., 2013). Due to these limitations, earth system models should take greater advantage of empirical relationships between climate and forest mortality to bridge knowledge gaps in mechanistic understanding, as global climate projections that incorporate biophysical feedbacks from forest loss are urgently needed for policy decisions. We encourage use of hybrid models and model ensembles that span the empirical to process-based continuum of approaches. Relatively empirical approaches, such as models based on FDSI-mortality correlations, could provide for rapid model development in tree mortality prediction.

Nevertheless, we do not advocate ceasing process-based model development. Inclusion of process-based representation for tree mortality mechanism has the potential to deliver more accurate projections if causal relationships are better understood. Moreover, even if parameterization for global process-based models is not possible in the near future, process-based models at fine scales may inform development of broader-scale empirical models through their ability to account for drought-driven changes in forest composition and distribution. We suggest several steps towards development of process-based, mechanistic models: (1) improved experimentation to distinguish physiological causes from symptoms, (2) continued model development based on existing knowledge and emerging discovery, (3) improved model validation against both experimental results and regional-scale mortality observations, and (4) high-resolution measurement of forest composition at large scales. While ecologists studying tree mortality have favored investigating physiological mechanism, measuring species composition and mortality at high resolution across regions

is crucial for providing baseline observations to constrain model predictions. Without improved input on current forest conditions, even accurate models of forest mortality cannot generate useful predictions of change.

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