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SYNTHESIS & INTEGRATION

Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models

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Abstract. Broad-scale forest die-off associated with drought and heat has now been reported from every forested continent, posing a global-scale challenge to forest management. Climate-driven die-off is frequently compounded with other drivers of tree mortality, such as altered land use, wildfire, and invasive species, making forest management increasingly complex. Facing similar challenges, rangeland managers have widely adopted the approach of developing conceptual models that identify key ecosystem states and major types of transitions between those states, known as "state-and-transition models" (S&T models). Using expert opinion and available research, the development of such conceptual S&T models has proven useful in anticipating ecosystem changes and identifying management actions to undertake or to avoid. In cases where detailed data are available, S&T models can be developed into probabilistic predictions, but even where data are insufficient to predict transition probabilities, conceptual S&T models can provide valuable insights for managing a given ecosystem and for comparing and contrasting different ecosystem dynamics. We assembled a synthesis of 14 forest die-off case studies from around the globe, each with sufficient information to infer impacts on forest dynamics and to inform management options following a forest die-off event. For each, we developed a conceptual S&T model to identify alternative ecosystem states, pathways of ecosystem change, and points where management interventions have been, or may be, successful in arresting or reversing undesirable changes. We found that our diverse set of mortality case studies fit into three broad classes of ecosystem trajectories: (1) single-state transition shifts, (2) ecological cascading responses and feedbacks, and (3) complex dynamics where multiple interactions, mortality drivers, and impacts create a range of possible state transition responses. We integrate monitoring and management goals in a framework aimed to facilitate development of conceptual S&T models for other forest die-off events. Our results highlight that although forest die-off events across the globe encompass many different underlying drivers and pathways of ecosystem change, there are commonalities in opportunities for successful management intervention.

Key words: climate change; conceptual state-and-transition models; drought; fire; forest management; pests and pathogens; tree die-off.

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Introduction

Forest die-off—a broad-scale tree mortality event—driven or exacerbated by drought and heat has now been reported from every forested continent (Allen et al. 2010). Forests sustain global biogeochemical cycles, providing vital habitat, and ecosystem services for human communities through the production of fiber, provision of water, and other economic or cultural resources. Understanding the drivers, patterns, and severity of changes to these critical functions is essential to minimizing their economic and cultural impact. Ecosystem changes during and following these events are a function of mortality drivers or sequences of environmental stresses, management, and/or biological agents that drive patterns of tree mortality across species and under different ecological or historical conditions (McDowell et al. 2011, Allen et al. 2015). However, forest die-off is playing out at the global scale and thereby encompasses a great diversity of underlying environmental stresses, biological agents, historical dynamics, ecological contexts, and the attendant interactions that drive these events. This complexity represents a serious challenge to developing a rapid understanding of why a particular mortality event has emerged as well as devising a sensible response with limited resources. Forest die-off is a daunting research and management challenge that is developing along with a growing consensus that it will increase as climate change progresses (McDowell et al. 2011, Adams et al. 2013, Hicke and Zeppel 2013, Weed et al. 2013, Allen et al. 2015, Anderegg et al. 2015, Millar and Stephenson 2015). Proactive science and management that develops tools useful for reducing the impacts of these events may be critical to maintaining resource provisioning in many forests (Millar and Stephenson 2015).

The ecological consequences of tree mortality are diverse and substantial, including changes in forest composition, structure, and function. For example, previous studies have identified changes to timber production, nutrient cycling and carbon sequestration, fire dynamics and intensity, and other impacts on ecosystem goods and services resulting from local-to-regional-scale forest die-off (Breshears et al. 2011, Anderegg et al. 2013, Norton et al. 2015, Ruthrof et al. 2016). A proactive management response is needed in the face of these threats, but, when viewed at the global scale at which forest die-off events are distributed, this response must be sufficiently flexible to encompass the diversity of drivers and impacts.

The scale and severity of many forest die-off events are of sufficient magnitude that management to effectively mitigate their impacts is difficult. The resultant challenges are intensified because many climate change-associated mortality events may lead to non-analogue states that emerge from novel environmental conditions and uncertainties associated with subsequent plant community changes (Williams and Jackson 2007, Millar and Stephenson 2015). Given the rate and extent of these mortality events, many land management agencies and forest stakeholders will face challenges that occur at a rate and extent that overtaxes resources (MacCleery 2008, Allen et al. 2015). These conditions suggest effective responses must help prioritize goals, have capacity for rapid application, and provide the feedback learning structure of adaptive management. However, to be useful at the global level, these tools must also accommodate the uncertainty associated with mortality events including potential non-linearity or threshold dynamics, initially unclear cause-and-effect relationships, and potential for non-analogue states.

Forest die-off during drought and the associated changes in forest structure, composition, or function are frequently driven or magnified by a range of familiar biotic or abiotic disturbances. These mortality drivers challenge managers in their own right and include insect or disease outbreak, land-use change, fire or fire suppression, and their interactions (Galiano et al. 2010, Metz et al. 2011, Weed et al. 2013). Often, these are endemic forces capable of structuring landscapes at spatial and temporal scales matching those of drought and heat events. These factors may also determine the magnitude, frequency, and extent of tree mortality resulting from climate dynamics such as drought and/or heat as well as the suitability of actions to reduce mortality or restore effected ecosystems (Harris et al. 2006).

Facing similar challenges of ecosystem changes in response to complex and interacting drivers, rangeland managers have pioneered, refined, and widely adopted the approach of developing conceptual models that identify key ecosystem states and major types of transitions between those states—known as "state-and-transition (S&T) models" (Westoby et al. 1989, Bestelmeyer et al. 2003, Stringham et al. 2003, Briske et al. 2008). While S&T models are frequently applied in rangeland ecology and management, including for semi-arid woodlands and forests, they have not gained widespread use in forest ecology and management (Bestelmeyer et al. 2003, Czembor and Vesk 2009). Using expert opinion in conjunction with available research, the development of such conceptual S&T models has proven useful in anticipating ecosystem changes, identifying management actions to undertake or to avoid, and directing data collection to key biological processes (Westoby et al. 1989, Miller 2005, Czembor and Vesk 2009). Where data and understanding are sufficient, S&T models can be developed into probabilistic simulations. However, even where data are insufficient to predict transition probabilities, conceptualizing key states, phase changes within states, and transitions can provide valuable insights for management by creating a basis to compare and learn from different ecosystems and point to key data needed to estimate threshold phenomena that govern both desirable and undesirable transitions (Stringham et al. 2003, Miller 2005, Briske et al. 2008).

We aimed to address challenges associated with ecosystem dynamics and management following forest die-off by developing a framework for synthesizing insights from case studies around the globe. We compiled a set of 14 globally distributed case studies that encompassed a broad range of climatic zones, species composition, and biological diversity. Each of our 14 case studies was placed into the framework of a conceptual S&T model (Westoby et al. 1989, Bestelmeyer et al. 2003, Briske et al. 2008) that described ecosystem states, associated transitions, and management options for system dynamics following forest die-off. This approach has aided rangeland management by providing a lens for viewing states as dynamic ecosystems, identifying reversible transitions, and describing pathways to restore structure or function when transitions are not directly reversible (Westoby et al. 1989, Stringham et al. 2003). We highlight the adaptive management utility of this approach by illustrating actions to minimize undesirable ecosystem changes such as conversion of forest to shrubland, loss of unique forest structure, impacts to timber growth, and hazardous accumulation of fuels. Our aim was not to conduct a comprehensive meta-analysis of climate change-driven mortality itself. Nor did we focus on developing specific probabilities for transitions between states, given that this would greatly limit the number of case studies across the globe that we would be able to consider; for most die-off events, in particular most unforeseen future events, these critical data are not available. Rather, we use our diverse set of case studies to (1) synthesize knowledge example-by-example to develop individual conceptual S&T models of forest ecosystem dynamics and management options following forest die-off events, (2) identify commonalities across the conceptual S&T models, and (3) use these insights to integrate a common set of research questions and monitoring goals in an adaptive management framework. The framework also serves as a roadmap for researchers and managers to create a conceptual S&T model for an emerging forest die-off event.

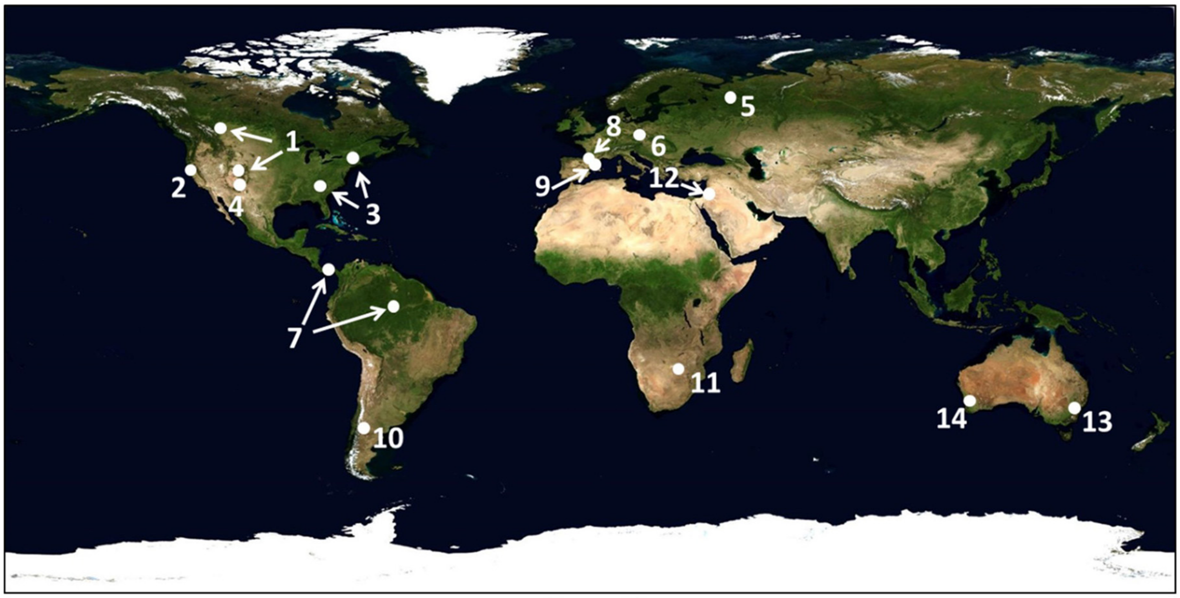
Forest Die-Off Case Studies

Our 14 forest die-off case studies have a global distribution and include tropical, temperate, Mediterranean, semi-arid, and boreal ecosystems (Fig. 1; Appendix S1). We included die-off events where the role of climate, specifically precipitation and/or temperature, as driving or contributing factors, was established. This decision excluded several forest die-off events driven directly by fire, disease, and land-use management practices. Our methodological approach required that each case study considered three criteria: (1) A series of ecosystem states and transitions could be quantified with vetted datasets and associated analyses (i.e., published in peer-reviewed journals), (2) mechanistic uncertainties associated with transitions—specifically transition thresholds (Stringham et al. 2003)—did not preclude inclusion in a given case study as long as the case study included ongoing or proposed experimentation to address these uncertainties, and (3) the example included ongoing or proposed management aimed at reducing die-off and conserving threatened ecosystem functions (Appendix S1).

Our case studies include nine from Northern Hemisphere forests in North America and Europe. Of these, six are located in conifer-dominated systems (six Pinaceae species and *Juniperus monosperma*), while the three others are in broad-leaved dominated systems (two Fagaceae species and *Populus tremuloides*). The Southern Hemisphere case studies are dominated by broad-leaved native tree species including three Myrtaceae species, *Colophospermum mopane* (Fabaceae), and *Nothofagus dombeyi* (Fig. 1). We included a single case study from the Neotropics that used two sites (Panama and Amazon Basin) where multiple species are impacted. Although this single tropical case study by no means encompasses the great diversity and variation in ecosystem dynamics relevant to tropical forests, this example met our inclusion criteria and the exercise identified actions with potential to improve management.

Differences in mortality drivers, ecological responses, methods of measurement, and experimental approaches among die-off events preclude many data synthesis techniques. As noted above, we therefore developed conceptual S&T models to describe mortality and response dynamics along with potential mitigating actions. S&T models provide a platform for linking processes of ecosystem change with different levels of confidence, identifying particularly important areas of uncertainty, and developing reasonable predictions of alternative ecosystem states (Bestelmeyer et al. 2003, Czembor and Vesk 2009). Conceptual S&T models are useful for guiding management decisions, describing ecological dynamics, as an aid to identify testable hypotheses, and as a dynamic tool to support adaptive management. S&T models are dynamic, meaning that as mechanistic drivers of mortality and types of responses are identified, the models can be revised and improved by adding or removing components, as well as parameterizing the strength, direction, and thresholds of transitions.

Building conceptual S&T models involves engaging a suite of expertise to define communities and community trajectories of change, and then defining states and transitions "based on postulates of vegetation change in combination with empirical observations of community structure and environmental change" (Bestelmeyer et al. 2003). Although less widely applied to forest ecosystems, the flexibility and low cost of applying conceptual S&T models suggest that they can be readily applied to forest die-off events that have very different sets of interacting drivers, species impacted, and local management goals. For the case studies included in this paper, our specific process of constructing a conceptual S&T model included three steps: (1) describing



Legend

Case study description	Case study Number	Transition Type	Species effected
Sudden Aspen Decline	1	Single	*Populus tremuloides* Mich:
Sudden Oak Death	2	Single	*Notholithocarpus densiflor* *Quercus agrifolia*
Hemlock woolly adelgid	3	Single	*Tsuga canadensis*
Ponderosa–piñon–juniper mortality	4	Cascade	*Pinus ponderosa*, *P. edulis*, *Juniperus monosperma*
Boreal spruce mortality	5	Cascade	*Picea abies* L. Karst.
Norway spruce beetle outbreaks	6	Cascade	*Picea abies* L. Karst.
Tropical forest fragmentation	7	Cascade	26 tree species impacted
Mediterranean Scots pine mortality	8	Complex	*Pinus sylvestris* L.
Holm oak mortality	9	Complex	*Quercus ilex* L.
Northern Patagonian	10	Complex	*Nothofagus dombeyi*
African savanna woodlands	11	Complex	*Colophospermum mopane*
Yatir forest	12	Complex	*Pinus halepensis* Mill.
Australian eucalyptus forests	13	Complex	*Eucalyptus maculata*
Eucalyptus marginata die-off	14	Complex	*Eucalyptus marginata*, *Corymbia calophylla*

Fig. 1. Distribution of our case studies used to assemble an adaptive management framework for climate change-driven forest die-off. Each case study including an appropriate state-and-transition model is reported in detail in Appendix S1. Some examples include multiple mortality locations. Background image source: NASA's Blue Marble.

specifics of the forest community including historical dynamics, (2) assessing the strength of biological, historical, or environmental mortality drivers, and (3) synthesizing existing results from management experiments or identifying data-driven potential management actions. We collectively used datasets, analysis, and inference to build conceptual models and recommend a similar approach to groups seeking to build an analogous model for an emerging die-off event. We were able to develop conceptual S&T models for 14 diverse forest die-off case studies. We integrated the examples by placing them into one of three related trajectories of ecosystem change: (1) single-state transition shifts, (2) ecological cascades, and (3) complex dynamics.

Single-State Transition Shifts

Three of our case studies fit into a simple category with a single-state transition (Fig. 2). Here, ecosystem change is a unidirectional shift which can result in a stable but novel ecosystem state. In each of our representative case studies (1–3; Fig. 1), ecosystem structure and function were altered, resulting in resource degradation (see additional detailed information in Appendix S1). Our examples included one case of sudden aspen decline (Anderegg et al. 2012), where climate was the primary mortality driver, and two examples of mortality driven by invasive biotic agents—sudden oak death and hemlock woolly adelgid (*Adelges tsugae*), where pest or pathogen invasion rates and impacts were the key driver of ecosystem change. In these invasive species examples, ecosystem impacts were modified by temperature and/or precipitation (Cobb et al. 2012, Orwig et al. 2012; Fig. 2). The single transition categorization by no means suggests that these systems are free from other sources of mortality or that mortality drivers were a function of a single factor. Further, forests are dynamic ecosystems shaped by a range of disturbances and environmental factors (cf. Westoby et al. 1989). In these examples, ecosystems shifted from one clearly identified state (species composition or forest structure) to another ecosystem state with readily identifiable differences where reversal to the initial state is extremely unlikely without a substantial input of energy (Fig. 2). Using the language of a conceptual S&T model, mortality drivers have pushed the system across a threshold that is not reversible without external effort, such as ecosystem restoration treatments. For example, sudden oak death (caused by the pathogen *Phytophthora ramorum*) occurs in an environment where fire is a major factor structuring ecosystems (Metz et al. 2011), but recent severe mortality and changes in structure and function are driven by pathogen invasion, a condition that does not appear to be reversible. In this system, local and regional

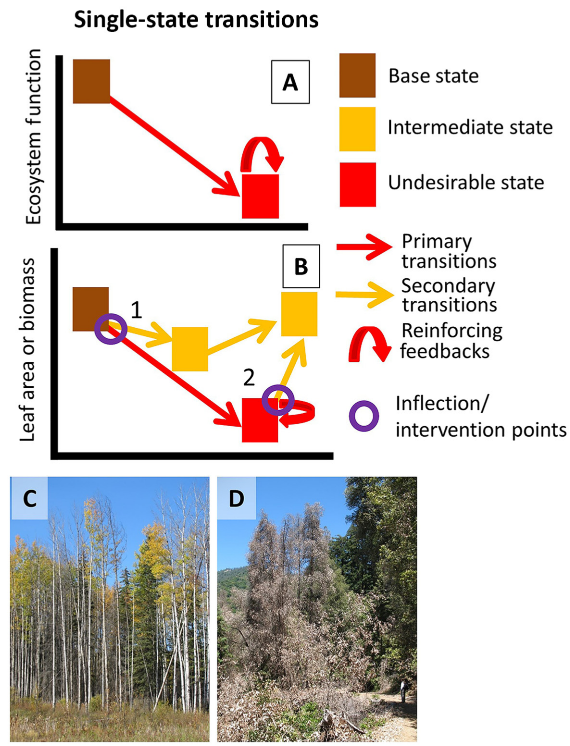


Fig. 2. Single-state transitions—mortality events distinguished by the overwhelming effect of a single factor. In the idealized example (A), a single event or driver forces the system into an undesirable state with positive feedbacks that maintain this condition. In several representative case studies (B), preventative management such as thinning or pathogen eradication (B-1) or restoration of degraded systems (B-2) ameliorates the loss of ecosystem function. Two examples from our case studies include sudden aspen decline (C), a climate-driven event where restoration is a feasible management option, and sudden oak death (D), where management focuses on restoration of degraded systems (case studies 1 and 2 respectively). Photo (D) courtesy of K. Frangioso.

climate variations in precipitation and temperature drive pathogen sporulation rates, infection, and tree mortality (Cobb et al. 2012). Above-ground biomass of *Notholithocarpus densiflorus* is killed by the pathogen but below-ground structures survive and resprout prolifically creating a transition from hardwood forest to dense shrubland punctuated with occasional overstory trees. This change in state is likely to persist for at least several decades without management intervention (Cobb et al. 2012). Similarly, tree harvest, native insects, and pathogens are important causes of eastern hemlock (*Tsuga canadensis*) mortality in New England but the invasive hemlock woolly adelgid is the main cause of tree mortality and the key driver of state transition across a large portion of the hemlock range (Orwig et al. 2012). Spread and impacts of this invasive insect are constrained at the landscape scale and within stands by year-to-year variation in minimum temperatures that, in turn, determine the severity of insect-caused hemlock mortality and ecosystem conversion into hardwood-dominated forests (Orwig et al. 2012). Hemlock woolly adelgid populations are sensitive to minimum winter temperatures; should these temperatures increase, impacts are expected to increase throughout New England (Orwig et al. 2012). In both of these cases of pest or pathogen invasion, the severity of ecosystem impacts and degree of ecosystem change are controlled by multiple factors, but the loss of a key overstory species is the primary driver of a single ecosystem state change.

Sudden aspen decline is similar to the previous two examples in that loss of a key overstory species also results in single ecosystem state change. However, sudden aspen decline is also noteworthy among all of our case studies in that precipitation and temperature are primarily responsible for die-off through direct effects of drought and heat on the physiological status and mortality rate of aspen (*Populus tremuloides*). Sudden aspen decline can lead to the loss of aspen overstory and subsequent clonal regeneration from buried buds on the root system (sucker regeneration), resulting in long-term changes to community structure and composition up to a complete loss of aspen and an increased dominance of shrubs or grasses, in some cases leading to non-forest vegetation types (Anderegg et al. 2012, Landhäusser and Lieffers 2012).

Management of single-state transition events appears deceptively simple, yet each of our examples this conceptual S&T structure included causes (climate change, species invasion) that are beyond the capacity or scale of local management actions. Despite this, identifying a mortality event as a single-state transition may still facilitate focus and prioritization of management actions. In our examples, identifying resilient overstory species is a research and monitoring strategy with potential to reduce impacts or restore degraded stands (Fig. 2). For other die-off events with a single-state transition, management applied prior to a die-off event may very well be more effective. This highlights both the potential and limitation of a conceptual S&T model: These are tools to develop a mechanistic understanding of mortality drivers and the capacity of management to address these changes. Synthesis of the conceptual model is a first step for actually acquiring that understanding, which in turn provides the parameterization and structure of predictive simulation models to forecast mortality risk and direct specific treatment applications.

Ecological Cascades

Four of our mortality case studies fit a S&T model comparable with the concept of an ecological cascade (cf. Allen 2007). Here, a set of state changes was driven by a progressive set of disturbances and the pool of species available to establish under changing biophysical conditions (Cornell and Harrison 2014). In our mortality case studies that fit this S&T model, ecosystem change was characterized by a single trajectory where multiple state transitions were responsible for the current ecosystem state (4–7; Fig. 3). In our examples, progressive environmental change led to the dominance of several different tree species or even ecosystem types (states) over the course of decades. For example, in our case study from the southwestern United States, semi-arid conifer forests have experienced continuous transitions of dominant tree species: from dominance of ponderosa pine (*Pinus ponderosa*), to co-dominance of piñon pine (*Pinus edulis*) and to sole dominance of juniper (*Juniperus monosperma*) over the course of 50 yr (Breshears et al. 2005, Allen 2007, case study 4). In this example, climate-driven changes

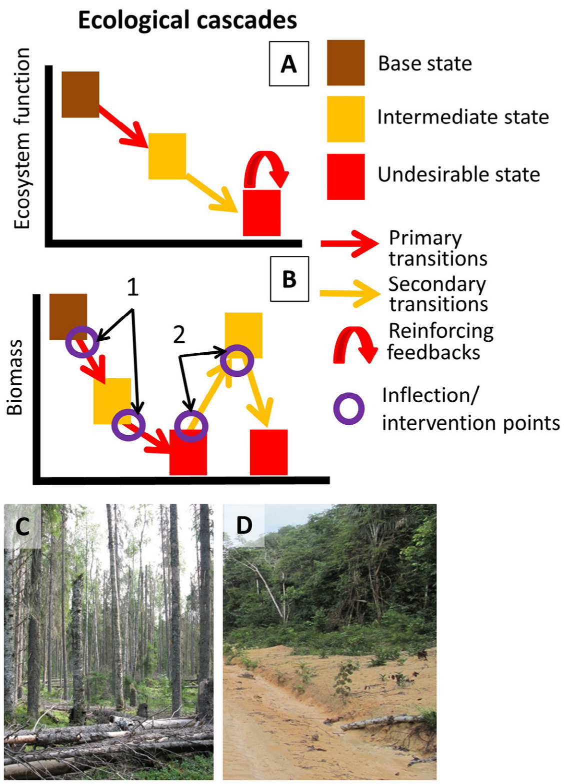


Fig. 3. Ecological cascades—mortality events involving multiple intermediate states. This class can also include oscillating dynamics that may increase in frequency with climate change. In the idealized example (A), a progression through one or more intermediate states leads to stabilization in an undesirable condition. In our case studies (B), multiple points of intervention occur (B-1, B-2) and encompass case-specific management actions. Increasing forest structural complexity can reduce frequency and intensity of native bark beetles outbreak (C; case studies 5 and 6). Better road planning and reforestation of roadside habitat with drought-tolerant trees could increase local system resiliency in road-impacted Neotropical systems (D; case study 7).

were so severe that the ecosystems are likely to transition into non-forest state in some areas that will not be easily reversed (Allen 2007). In contrast to this system, in our other three cascade examples, the system could revert to an initial state, such as a late-seral conifer forest structure. In these cases, re-occurring climate and biotic drivers of mortality forced the system through a progressive set of conditions that oscillated between two or more ecosystem states. For these cases, the change in state is the degree of oscillation and the severity of mortality, loss of function, or change in structure. In two case studies of spruce bark beetle (*Ips typographus*) attacks in Norway spruce (*Picea abies*) forests, outbreaks followed a cycle of forest growth and explosive insect outbreak. Here, outbreaks were driven by the interaction of climatic conditions and management actions, especially even-age forest structure or a homogeneous species composition (Aakala et al. 2011, Temperli et al. 2013, case studies 5 and 6). In contrast to the semi-arid forest example from North America, these ecosystems often recover to their initial species dominance, but management actions and climate change appear to be increasing the magnitude of mortality during beetle outbreak. Our sole case study of tropical forest die-off is another example of an ecological cascade. Here, road construction increases dominance of drought-intolerant species along roads, which leads to greater mortality during drought episodes (Kunert et al. 2015, case study 7). Increases in drought frequency and severity are likely to interact with road construction to create state changes that are unlikely to reverse without management effort. Collectively, our ecological cascade case studies suggest that increased rates of state changes or increased magnitude of oscillations between states could lead to a loss of biodiversity and resilience (see also Johnstone et al. 2016).

Management in these ecological cascade examples could be effective by targeting individual transitions that are well understood and for which practical interventions are possible. For example, in the spruce beetle examples, silvicultural treatments that increase species or age diversity are likely to dampen subsequent spruce beetle outbreaks and associated mortality, even in the face of future drought (Aakala et al. 2011, Temperli et al. 2013). In the semi-arid forest example, accounting for grazing impacts and reintroducing fire could reduce tree mortality or prevent loss of forested conditions under some circumstances (Allen 2007). In the tropical example, integration of forest dynamics and mortality vulnerability into road planning could help reduce tree mortality and refine cost–benefit analyses of infrastructure development in tropical forests. Similar to the single-state transitions (Fig. 2), drought and perhaps other environmental factors are outside of the scope of control for local managers, but understanding patterns of mortality provides the foundation to address ecological impacts. Identifying a die-off event as an ecological cascade carries the implication that multiple points of intervention may be possible.

Complex Dynamics

Seven of our case studies fit a multi-pathway trajectory of ecosystem change that was the most complex and most frequent response framework that we identified. These examples have at least one state that can transition to at least two alternative states independent of a management action (8–14; Fig. 4). Alternative states were contingent on many, and sometimes interacting, tree mortality drivers, including land-use history, biotic agents such as insects and pathogens, fire, or climatic factors. Single-state transitions and ecological cascades can be encompassed within these examples, and a host of contingent processes or disturbances can shift ecosystem trajectory as well as the severity of impacts. To construct our conceptual S&T models for these case studies, many ecosystem states, transitions, and points of management intervention needed to be evaluated (Fig. 4). We expect that the process for constructing conceptual S&T models for emerging mortality events will be comparably complex and that the full scope of interactions, states, and transitions may only emerge over time with careful monitoring.

Despite their complexity, we were able to construct conceptual S&T models for disparate and often complicated or nuanced die-off events. For example, in our Holm oak case study (*Quercus ilex*, case study 8), the degree of drought-induced forest die-off was dependent on soil depth. Mortality also influenced fuel accumulation, which, in conjunction with fire and soil erosion (a process that reduces soil depth), influences forest recovery and the degree of severity of future mortality events. Multiple points of potential management were identified in this conceptual S&T model, but it is also clear from the existing data that local ecological context has a strong influence on the success of management to reduce mortality. In another example, the degree of African savanna drought-driven tree mortality (case study 11) was dependent on historical grazing intensity. Initial tree mortality and factors influencing grazing, particularly policy actions that led to the construction of supplemental wildlife water sources, determined the degree of ecosystem change and the temporal duration of some ecosystem states. Here, grazing and climate (drought) also determined the cost and success of forest restoration treatments, as well as the potential for persistent loss of woody vegetation.

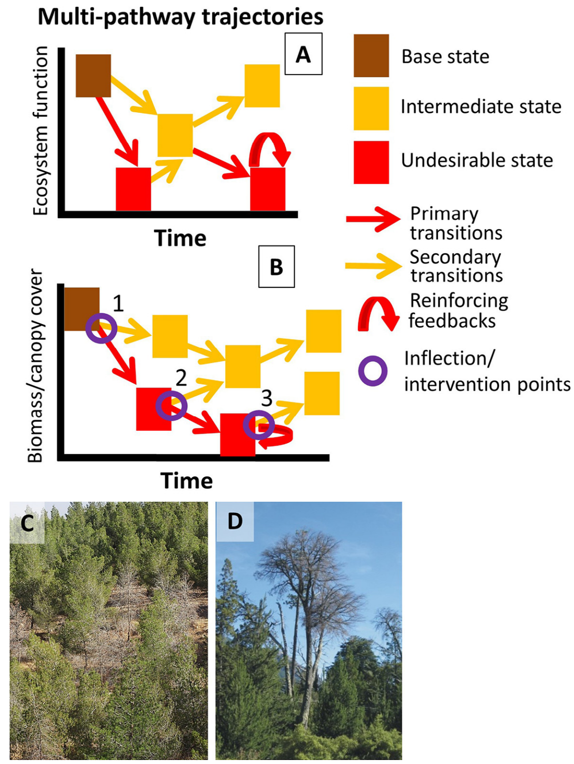


Fig. 4. Complex dynamics—mortality events that include multiple potential transitions at one or more states (A). In our case studies (B), key intervention opportunities or transitions (B 1–3) occur at several ecosystem states and often involve interactions between drought and management actions. Grazing and thinning determine whether fire, drought, and shrub establishment lead to loss of *Pinus halepensis* forests in the Yatir region of Israel (C; case study 12). Repeated drought along with fire and shrub encroachment drives long-term vegetation dynamics in *Nothofagus dombeyi–Austrocedrus chilensis* forests (D; case study 10) and suggests restoration with drought-tolerant species may help maintain forest structure over the long term.

Complex dynamics are clearly the most difficult to anticipate or manage. It is likely that progressive experimentation will be needed to push understanding of these systems to subsequent stages where predictive models and more optimal management are possible. The structural variability of these examples cautions against over-generalization from one or a few case studies, and we again acknowledge that the conceptual models we present here can and should change over time as understanding develops. For example, in the Yatir (Israel) forest case study—one of the most arid forests in the world—management involving thinning was found to increase stand biomass and decrease drought-associated mortality in Aleppo pine (*Pinus halepensis*) plantations (10; Klein et al. 2014*a*, *b*). Wildfire and managed grazing are contingencies that determine transitions into various alternative ecosystem states, some undesirable, through effects on sapling survival and establishment. In order to maintain a forest state, grazing levels must be monitored and adjusted according to drought dynamics. These contingencies and ecosystem dynamics became clear over years of integrated management and research efforts, illustrating how conceptual S&T models are dynamic tools that rely on constant updating and revision but which can improve resource sustainability (Briske et al. 2008). In our Scots pine (*Pinus sylvestris*, Iberian Peninsula) example, changes in land use and land management policy over the last century led to increased afforestation. However, significant mortality in pine plantations and recently pine-invaded lands has emerged due to interactions among competition, pathogens, and drought (case study 9; Galiano et al. 2010, Camarero et al. 2011). Heterogeneous risk is associated with a variation in soil texture and its control on water availability as well as the effect of thinning treatments on competition for soil water. This example illustrates how mortality risk, underlying drivers, and management efficacy can change over time. Continued climate shifts toward warmer and drier conditions are expected within the region (Galiano et al. 2010), implying the conceptual S&T model, and any predictive model, will be improved by integrating additional sources of information such as regional climate change forecasts.

Fire was a frequent mortality driver within our case studies with complex dynamics. Fire acted to alter ecosystem states and trajectories by directly causing mortality (case studies 10 and 11), restricting regeneration, or affecting individual tree resilience to subsequent drought (case studies 12 and 13), or through mortality–fire interactions via fuel accumulation (case studies 9 and 11). That fire was a frequent component of these examples is unsurprising, given the importance of fire in shaping the structure, composition, and function of many forests across the globe. However, many of the other mortality drivers could interact with fire in ways that influence mortality during fire. Mortality-driven fuel accumulation is likely a common impact of climate change-associated mortality events, but the importance of these fuels can also be nuanced and system specific. Canopy fuel levels and the timing of fire have critical influences on fire behavior and severity to the point that depletion of canopy fuels during mortality events could lead to a reduction in fire severity (Simard et al. 2010, Metz et al. 2011). Fuel accumulations are often a focal point of public attention and management efforts because of concerns regarding fire-caused mortality and the cost of fire control activities. Although these concerns may be justified in some cases, there are few studies that directly address fire–disturbance interactions, meaning that predictions to their magnitude and ecological importance have a weak basis (Simard et al. 2010, Metz et al. 2011, Johnstone et al. 2016). This is a research and management problem that could have growing importance as overlap between climate-related die-off and fire becomes more common (Anderegg et al. 2013).

The case studies with complex dynamics also highlight the challenge that management can be a solution or contributor to mortality dynamics. Several vegetation transitions were associated with, or exacerbated by, management such as planting species at their range limit (case study 8; Galiano et al. 2010), increased ungulate populations following construction of watering holes (case study 11; Thrash 1998), or interactions of overgrazing, vegetation change, and/or soil erosion (case studies 9, 11, and 12; Macgregor and O'Connor 2002, Lloret et al. 2004). Furthermore, many management policies may appear completely reasonable under current climate and resource conditions but prove to be problematic in the face of dynamic and rapidly changing environmental conditions (Milly et al. 2008, Breshears et al. 2011). The solution to this problem is, in part, a commitment to experimental evaluation of management actions. When using conceptual S&T models, this involves revisiting and improving the model assumptions including the number of potential ecosystem states, the strength and direction of the transitions, and thresholds that govern state transitions.

Adaptive Management of Climate-Driven Mortality Events

Our overarching goal was to use our case studies to synthesize knowledge, identify commonalities, and integrate our insights into a common set of research questions and monitoring goals in an adaptive management framework. Our additional motivation is to facilitate development of conceptual S&T models by researchers and managers confronting emerging mortality events across the globe. We constructed Fig. 5 as a

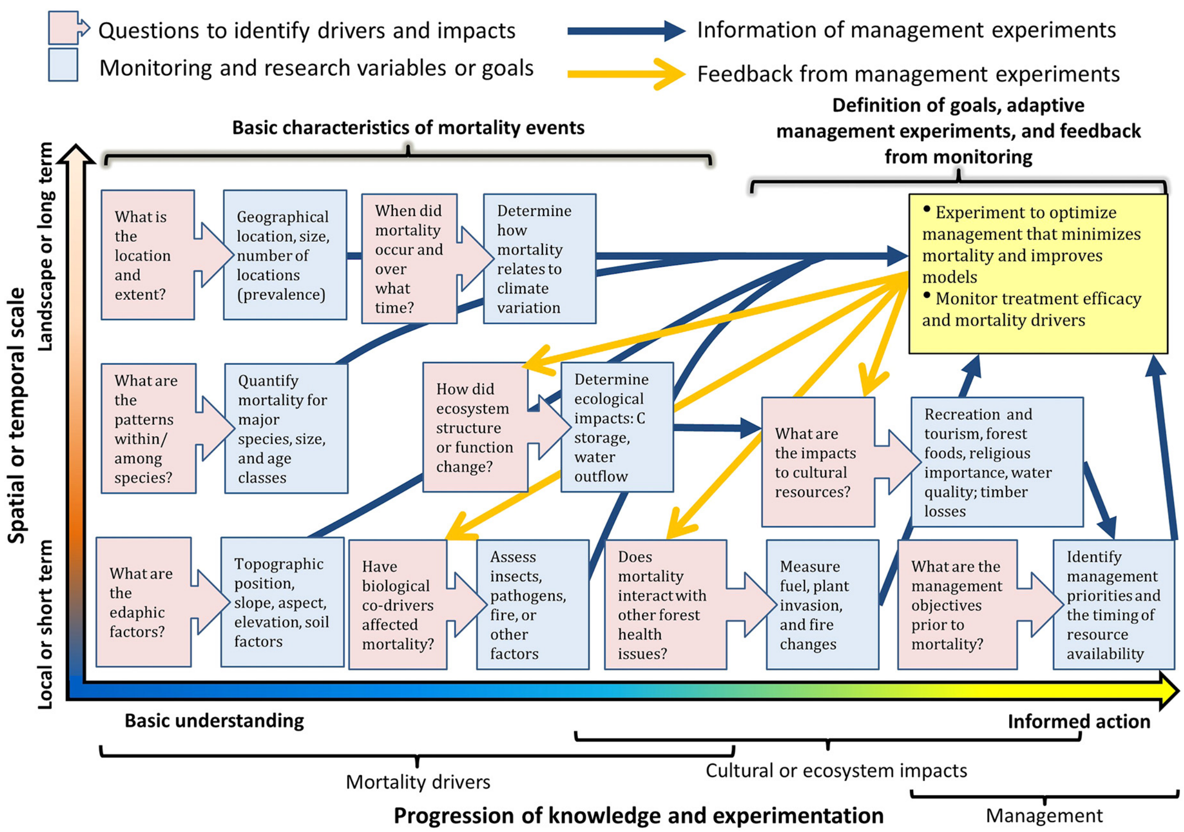


Fig. 5. A framework for understanding mortality drivers and identifying useful intervention in an adaptive management framework. Research questions and monitoring goals are integrated according to temporal/spatial extent (y-axis) and progressive understanding (x-axis). We suggest a division into three somewhat overlapping classes of research and monitoring goals (x-axis). The framework can be used to address an emerging mortality event by progressing from development of basic understanding at the stand scale (lower left-hand corner) to increased spatial extents. Simultaneously, better understanding of mortality drivers and impacts will lead to informed management experiments at the stand and landscape extents. This is an adaptive management framework where knowledge gained from experiments (blue arrows) is part of a feedback informing experiments (yellow arrows). In recognition of the multiple uncertainties that characterize emerging mortality events and the potential for multiple independent or interacting drivers, this framework is constructed as sets of questions (red boxes) to guide monitoring and research along with their respective goals for analysis (blue boxes).

condensed guide and model for S&T development; the figure represents questions and/or data that were necessary for constructing each of our conceptual S&T models. This list of questions or monitoring goals was then placed into the dynamic feedback of standard adaptive management models while also suggesting a progression of tasks to span basic understanding and informed action in a spatial or temporal context. Of course, our questions by no means encompass the full range of mortality drivers, ecological impacts, or management goals encompassed by the global context of these events. Instead, Fig. 5 represents a methodological tool for developing a conceptual S&T model, which in turn may be placed within one of the three general ecosystem responses we identified (single-state transition, ecological cascade, and complex; Figs. 2–4). Constructing conceptual S&T models may often be a reasonable goal given available resources and is more rapid than development of predictive models while also building their foundation (cf. Stringham et al. 2003). Our specific examples may additionally help speed application of management when responses fit one of our three ecosystem trajectories (Figs. 2–4) and when emerging mortality events can be understood with the specific questions and goals we used (Fig. 5). However, the process of constructing a conceptual S&T model is also likely to be of great value for researchers and managers addressing emerging events as the process can force a critical evaluation of evidence and assumptions, which in turn will direct data collection and potential management experiments.

Constructing Conceptual State-and-Transition Models for Emerging Events

Our experience suggests that constructing a conceptual S&T model will encompass relatively simple to relatively difficult research, monitoring, or management challenges. For example, some of the driving or contributing factors, such as the role of insects and pathogens, could be excluded quickly in cases where evidence for biological drivers is absent. However, a hypothetical case where mortality drivers are topographic factors and vulnerability among species or size classes culminating from years of environmental change is likely to require fairly detailed and long-term datasets to understand. Further, successional dynamics and delayed effects are difficult to assess due to their slow rates of change. However, this information may be essential as it informs forest restoration strategies and helps identify associated achievable goals (Harris et al. 2006, Cornell and Harrison 2014, Johnstone et al. 2016). Monitoring the timing and extent of mortality was a basic data requirement for all of our case studies, and we expect for almost all other emerging mortality events. These data are essential to assessing the degree of ecosystem resilience and detecting changes in stand structure that create a basis for further tree mortality from biological agents, fire, and other environmental stresses (Drever et al. 2006, Galiano et al. 2010, Aakala et al. 2011).

Assessment of the causes of past or ongoing mortality was inherent to building our conceptual S&T models and can also be valuable in synthesizing risk estimates for ecosystem transitions by helping to identify threshold phenomena across spatial scales (Adams et al. 2013, Johnstone et al. 2016). Reasonably designed monitoring and careful assessment of contributing factors can also clarify sources of uncertainty; in turn, these efforts have potential to overcome the problem of faulty preconceived notions of risk (McRoberts et al. 2011, Allen et al. 2015). Correct information on the nature of risks, as well as their immediate threat, is fundamental to communicating nuanced monitoring or counterintuitive treatments to stakeholders, as well as identifying tradeoffs inherent in many management actions (D'Amato et al. 2011, Hirsch et al. 2011). We expect that these efforts will often be aimed to go beyond the generalities of conceptual S&T models, specifically the development of mechanistic models, maps of vulnerability, and a prioritization of management resources (Klein et al. 2014*b*). If our case studies prove a useful guide for other emerging forest mortality events, we expect that identifying transitions, critical states and drivers, and realized impacts will also reveal testable hypotheses that can accelerate model development for specific purposes such as forecasting risk.

While our case studies rely on insights and experiments led by land managers and policy makers, the specific questions and goals rendered in Fig. 5 reflect the approach of research ecologists, the primary background, and profession of the authors of this article. However, the process of constructing a conceptual S&T model could be led by a professional forester working primarily at the unit of a forest stand or a policy maker working at the region, state/province, or international scale. Aspects of the process would be the same as presented in Fig. 5, with basic understanding providing the foundation for experiments and spatial or temporal context driving strategic decisions. Here, professional researchers would play a support role that ensures a strong biological or ecological foundation to a conceptual S&T model that is management or policy focused. We envision our own conceptual S&T models developing into a management or policy focus over time. As basic understanding of mortality drivers strengthens, informed action can be tailored to addressing specific thresholds or transitions and restoring or protecting specific ecosystem states. Much of the S&T model literature from rangeland management explicitly or in principle emphasizes this transition from developing a basic understanding to implementation of informed management actions (Bestelmeyer et al. 2003, Stringham et al. 2003, Briske et al. 2008). The approach could also benefit efforts to address the local impacts but global scale of tree mortality (Allen et al. 2015, Millar and Stephenson 2015).

Experimentation as a Driver of Conceptual Model Development, Detecting Bias, and Quantifying Uncertainty

Biologically underpinned management experiments should emerge from the basic understanding of mortality events (Fig. 5), but it is also helpful to acknowledge that good experiments can reveal optimal treatments that may be counterintuitive. In our hemlock woolly adelgid example (case study 3), salvage logging of uninvaded hemlock stands has accelerated the loss of this unique forest type in New England landscapes (Foster and Orwig 2006, Orwig et al. 2012). These actions accelerate the loss of landscape-level biodiversity, one of the most problematic consequences of invasion by this exotic insect. Carefully designed, experiments applied at a sufficient spatial extent can show that "control" or "no-treatment" options may be optimal in some situations. If cutting, planting, burning, or other management actions result in greater mortality and greater loss of ecosystem function relative to an untreated control ("failed treatments"), this information can be valuable in refining where future experimental management efforts might be most effectively focused. Understanding and communicating this information is immensely valuable when highly visible forest die-off galvanizes public attention and mobilizes resources.

The broad term "thinning" encompasses many different silvicultural treatments aimed at manipulating size or age class distribution, species composition, and density. Treatments aimed at reducing stand density to specific targets was a widely used forest management tool in our set of case studies (4–5, 8–9, 12–13), and the effectiveness of thinning treatments in often reducing tree drought stress and increasing resistance to pests and pathogens has been demonstrated in many forests (Fettig et al. 2007, D'Amato et al. 2011). However, thinning can also increase mortality vulnerability, for example, when it results in increased growth of understory plants that provide tree pathogen inoculum sources (such as for white pine blister rust; Maloney et al. 2008), inadvertently enhancing pest populations by increasing slash (Fettig et al. 2007), or increasing windthrow (Temperli et al. 2013). Fire is often used to reduce stand density to promote forest health and is more cost-effective than mechanical tree removal in some systems. However, fire can also lead to increased tree vulnerability to drought and insect pests (Maloney et al. 2008). This variation in the effect of thinning treatments on ecosystem trajectories emphasizes the case-by-case context of factors driving forest die-off events.

Our case studies collectively also represent a common bias of ecological research: They tend to over-represent examples from developed nations and the Northern Hemisphere. More examples from tropical systems, nations with greater dependence on subsistence agriculture, other traditional forest uses, and greater variation in human population densities are likely to include management actions and goals different from our case studies. Further, developing understanding of mortality drivers, data collection efforts, and model revision are all likely to be more successful when these efforts integrate the leadership structures, insight

Table 1. Examples of management actions in response to forest die-off events with unintended and undesirable consequences.

Management action type	Potential unintended consequence	Example	Reference
No action	Maximum loss of cultural, ecological, or economic resources; difficult to reverse state changes	Most climate change mortality events	Allen et al. (2010)
Combined thinning and controlled burning targeted to reduce density and competition	Increased tree stress following thinning and burning predisposes trees to endemic pests and pathogens	Restoration in fire suppression-impacted forests	Maloney et al. (2008)
Species or genotype selection	Shift to maladapted genetic mixtures; increased susceptibility to mortality or likelihood of state change	Selection of species and genotypes in high-diversity tropical forests	Kunert and Mercado (2015)
Salvage logging of valuable timber in anticipation of mortality	Accelerated state change through loss of desired species, tree size classes, or soil resources	Salvage logging in forests at risk of insect outbreak	Foster and Orwig (2006) and Carver et al. (2009)
Even-age silviculture, especially plantation-style reforestation	State change to damaging oscillations of forest die-off	Norway spruce beetle outbreak	Aakala et al. (2011) and Temperli et al. (2013)
Replanting with alternative species	State changes due to introduction of invasive species, edaphic mismatch, and restoration failures	Many invasives introduced for erosion control, failed plantings	Harris et al. (2006)
Deprioritization of proactive treatments; reactionary management	Cycles of crisis; inefficient effort	US National Forest fire management	North et al. (2015)

into ecological processes, and cultural perspectives of local people (Lake et al. 2017). We argue that the overall synthesis and especially the framework for devising a conceptual S&T model for an emerging die-off event (Fig. 5) provide a useful starting point and that the collaborative nature of constructing these models could develop unique dialogue and collaboration with stakeholders in regions underrepresented by our case studies, yet still affected by tree mortality.

Recognition of uncertainty and acceptance that changing conditions and unforeseen events will sometimes overcome well-reasoned efforts is a critical assumption of adaptive management (Walters and Holling 1990). However, even "failed" management actions can be extremely informative when careful monitoring and analysis unveils mortality drivers hidden by context dependency (Maloney et al. 2008). For each management action type, additional mortality is a potential unintended consequence (Table 1). Many of these actions have positive benefits which may outweigh the unintended or unanticipated costs, particularly when viewed over longer time scales. Recognizing unintended consequences in a transparent manner will foster collaboration and cooperation among stakeholders and, in the ideal scenario, retain focus on the adaptive management process despite individual setbacks. Embracing the possibility that treatments may fail to meet the intended goal opens new pathways for discovery and improved actions. Further, unintended consequences are often a research and management opportunity given that unexpected mortality reflects inadequate or inaccurate understanding of how to mitigate mortality events. Lastly, a well-known premise of adaptive management is that static prescriptive action is very likely to be suboptimal. Rather, management will be a continuously evolving process built on feedbacks among biological understanding, experimentation, and dynamic ecosystems.

Conclusions

Forest die-off events are emerging as an ecological challenge across the globe and demand a framework for improving understanding of mortality drivers, ecosystem responses, and management. We gathered a set of globally distributed and diverse forest die-off case studies to develop conceptual S&T models, identified three general classes of ecosystem transitions, and placed the construction of these models within a traditional adaptive management framework for describing and responding to climate-driven forest die-off (Fig. 5). We found that we could place a diverse set of events within conceptual S&T models that revealed useful interventions across die-off events. We suggest that by applying this framework to emerging forest die-off events, managers, policy makers, and researchers can accelerate the development of case-specific models, management actions, and ultimately solutions. Given the frequency of drought-induced forest die-off events across the globe, and increasingly limited management resources, rapidly identifying effective treatments and intervention actions is essential to future forest management.

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