Commentary

Climate-driven tree mortality: insights from the piñon pine die-off in the United States

The global climate is changing, and a range of negative effects on plants has already been observed and will likely continue into the future. One of the most apparent consequences of climate change is widespread tree mortality (Fig. 1). Extensive tree die-offs resulting from recent climate change have been documented across a range of forest types on all forested continents (Allen *et al.*, 2010). The exact physiological mechanisms causing this mortality are not yet well understood (e.g. McDowell, 2011), but they are likely caused by reductions in precipitation and increases in temperatures and vapor pressure deficit (VPD) that lead to enhanced soil moisture deficits and/or increased atmospheric demand of water from plants. When plant stomata close because of a lack of available soil water or high atmospheric demand, the plant cannot photosynthesize (leading to carbon (C) starvation) and/or cannot move water from roots to leaves (hydraulic limitation); either mechanism reduces growth, potentially leading directly to mortality and/or to reduced capacity to defend against insect or pathogen attack. Regardless of the mechanisms, few studies have documented relationships between climate and large-scale tree die-offs. In this issue of *New Phytologist* (pp. 413–421) Clifford *et al.* address this gap by reporting on a study of climate conditions during widespread piñon pine mortality that occurred in the early 2000s. This die-off occurred across 1.2 Mha of the southwestern United States (Breshears *et al.*, 2005) and killed up to 350 million piñon pines (Meddens *et al.*, 2012; Fig. 2). A combination of low precipitation, high temperatures and VPD, and bark beetles was reported to cause the mortality (Breshears *et al.*, 2005).

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Clifford *et al.* focused on tree mortality along a 180-km transect across northern New Mexico, USA. The authors combined field observations at 95 plots and remotely sensed imagery to quantify tree mortality in this area, and related mortality to climate in 2002 and 2003. Key to this transect was a gradient of precipitation trends in which greater reductions occurred in the north than the south (the entire study area experienced warming). In addition to this climate gradient, a tree mortality gradient, which increased from south to north, was documented by both the field measurements and remote sensing.

Past studies have argued that quantifying thresholds of mortality are needed to allow us to predict which plants will be more susceptible to drought mortality (McDowell *et al.*, 2011; Zeppel *et al.*, 2013). Clifford *et al.* related cumulative 2002–2003 precipitation values to field measurements of tree mortality, finding a threshold of 600 mm for cumulative 2-yr precipitation, above

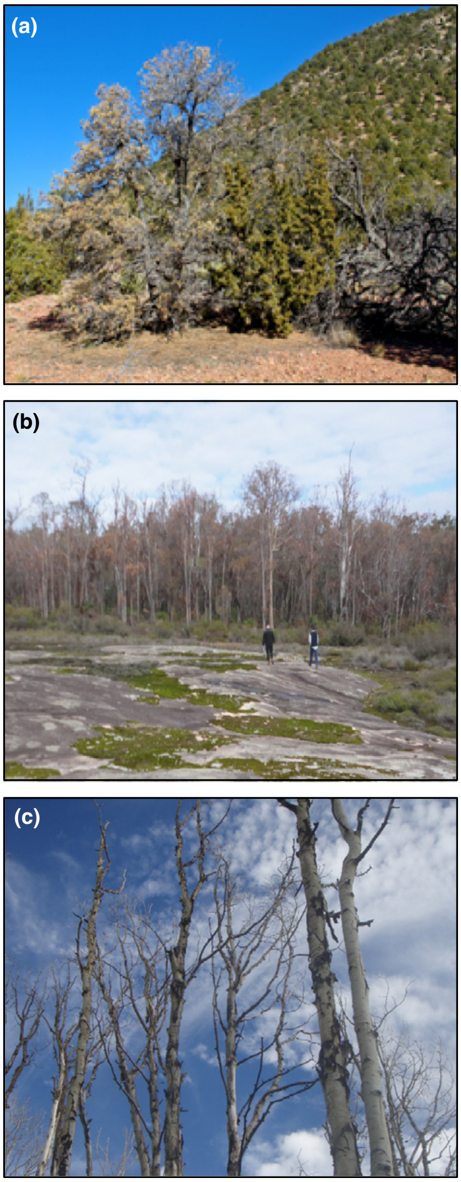

Fig. 1 Tree mortality during recent die-off events: (a) piñon pine, New Mexico, USA (photograph courtesy of A. Mack); (b) *Eucalyptus*, New South Wales, Australia (photograph courtesy of P. Mitchell); and (c) trembling aspen, Colorado, USA (photograph courtesy of W. Anderegg).

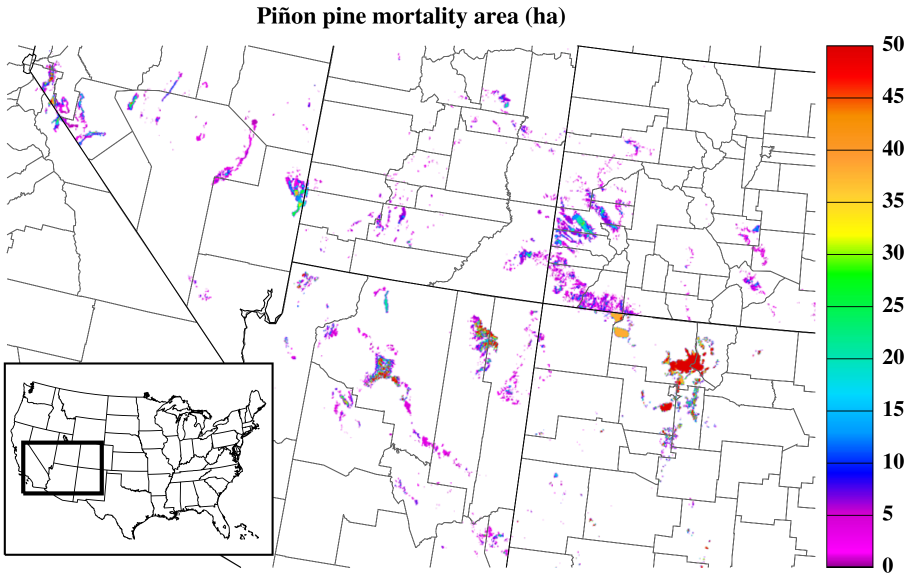

Fig. 2 Piñon pine mortality area in southwestern United States (ha within 1-km^2 grid cells) from the early 2000s (Meddens *et al.*, 2012).

which little or no mortality occurred. Conversely, substantial mortality occurred within some sites with < 600 mm. The authors also reported a VPD threshold of 1.7 kPa, above which sites experienced tree mortality. This VPD threshold contrasts with the threshold of 3.0 kPa for increased risk of mortality in the broad-leaf evergreen *Eucalyptus globulus* (Mendham *et al.*, 2005). The contrasting mortality thresholds for these conifers and broadleaf evergreens imply differences across plant functional types, and highlight the need for further research. Clifford *et al.* did not have any success modeling climate–stand structure–tree mortality relationships with linear regression, illustrating the complexity and perhaps nonlinear nature of the climate–plant relationships.

This study is novel for several reasons. The authors covered extensive spatial gradients in climate and tree mortality, using widespread field sampling in conjunction with remote sensing to examine variability along these gradients. A combination of methods including field observations of mortality and stand structure, remote sensing, and analyses of climate station and gridded climate data allowed them to ascertain climate influences on mortality. Multiple climate factors were considered that represented both soil moisture and atmospheric demand. Finally, the study used various analytical methods, including examining relationships with multivariate linear regression modeling (which produced insignificant results and low goodness-of-fit) and empirical analysis (which identified simple thresholds in precipitation and VPD).

The authors make significant contributions to understanding mechanisms of tree mortality. Yet the study also raises important questions. First is a set of questions related to the characteristics of the piñon pine die-off. How widely applicable are these results? Determining whether the reported precipitation and VPD thresholds are similar in other areas of piñon pine mortality and for other woodland tree species or other plant functional types is critical for successful modeling of other die-off events. How much stress can piñon pines (and other plants) undergo before succumbing to death? How long before a severely stressed tree recovers to 'normal' growth?

Second, important questions remain about the mechanisms causing tree mortality. What is the relative importance of reductions in precipitation vs increases in VPD? In their study Clifford *et al.* found substantial variability in tree mortality beyond the precipitation and VPD thresholds, and the authors were unsuccessful at modeling mortality with multivariate linear regression methods. What is the source of this variability? Clearly microsite differences contributed, but to what extent? What are the important predisposing factors that might be considered by future studies? Perhaps using variables that better represent drivers, such as modeled soil moisture or climatic water deficit, would yield improved relationships. The authors reported similar warming at the ends of their mortality gradient, suggesting that precipitation or humidity may have played more important roles than temperature in driving tree mortality.

Bark beetles were also an important factor in the piñon pine die-off (Breshears *et al.*, 2005). Climate influences beetle outbreaks through drought stress of host trees and accelerated beetle life cycles from higher temperatures. The beetle species involved, piñon ips (*Ips confusus*), does not kill healthy trees, unlike some other major bark beetle species. Instead, ips populations increase with drought stress and decline when drought is relieved (Raffa *et al.*, 2008; Gaylord *et al.*, 2013). Beyond this simple characterization, however, we lack the basic knowledge about the population dynamics of these beetles and interactions with climate change. Furthermore, we need a better understanding of the role these beetles played in this piñon pine die-off: what proportion of trees would have survived in the absence of beetles?

A third set of questions concerns predicting die-offs. What are the prospects for modeling future tree mortality given expected increased tree stress associated with future climate change (Williams *et al.*, 2013)? Models are urgently needed to inform resource managers, policy makers, and the public about which forests will be vulnerable to mortality in the coming decades. The findings of Clifford *et al.* on precipitation and VPD thresholds offer a first step toward predictions, yet the complexity of these relationships suggest challenges to building robust models. Other regions in western North America, Europe, South America, and Australia have experienced tree mortality as well. These other events have challenges of their own. Some cases, such as sudden aspen decline, appear to be primarily driven by physical climate changes (e.g. drought; Anderegg *et al.*, 2012), implying that modeling may be easier. Other cases, such as lodgepole pine mortality caused by mountain pine beetles, involve a combination of climate, beetle population dynamics, and host–beetle interactions (Raffa *et al.*, 2008), suggesting more complex modeling is required.

Significant challenges exist for obtaining useful data for analyses of tree mortality. Clifford *et al.* invested substantial time in measuring 95 plots, and similar intensive fieldwork will provide valuable information for future studies. Clifford *et al.* also used remotely sensed imagery to map mortality. Interestingly, the field data the authors used to build their remote sensing-based model covered only 1% of the imagery area at each location, yet the authors achieved good accuracy with their remote sensing-based model. Use of satellite imagery for mapping tree mortality is desirable for extending study areas, though tests of these methods to other regions are needed. Finally, Clifford *et al.* relied on gridded climate data at reasonably fine spatial resolution (4 km) to examine precipitation and VPD at their field sites. Such data sets work well for variables that generally vary smoothly in space, although patchier summer precipitation from convective storms, potentially important in delivering needed moisture to trees, may not be well represented. Furthermore, such fine-resolution data sets that vary in time cover only limited regions globally, yet studies of impacts in mountainous regions require fine detail to capture steep gradients in complex terrain.

Die-offs are significant events for humans and natural systems. Services to humans, biogeochemical cycling (including C and water), energy fluxes, and wildlife habitat are among the processes severely affected by die-offs (Breshears *et al.*, 2011; Anderegg *et al.*, 2013). Widespread tree mortality is an indicator of climate change clearly visible not only to scientists but also decision makers and the general public. Our ability to accurately predict how forests will respond to warming, and the impacts that will cascade through ecosystems, relies on our understanding of how climate influences trees. The Clifford *et al.* study advances this knowledge, suggesting and inspiring future studies that build from these results. However, the complexity of forest die-offs will challenge scientists to describe, explain, and model these events. Research is needed that: is interdisciplinary in nature, involves tree physiologists, forest and landscape ecologists, climatologists, and entomologists; covers a range of plant functional types and biomes; and considers multiple spatial scales, from leaves to whole trees to landscapes to the globe.

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