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Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback

Alistair S. Jump[1,2], Paloma Ruiz-Benito[1,3], Sarah Greenwood[1], Craig D. Allen[4], Thomas Kitzberger[5], Rod Fensham[6], Jordi Martínez-Vilalta[2,7] and Francisco Lloret[2,7]

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[1]Biological and Environmental Sciences, University of Stirling, Scotland, FK9 4LA, UK.

[2]CREAF, Campus de Bellaterra (UAB), Edifici C, Cerdanyola del Vallès 08193, Catalonia, Spain.

[3]Forest Ecology and Restoration Group, Department of Life Sciences, Science Building, Universidad de Alcalá, Campus Universitario, 28805 Alcalá de Henares, Madrid, Spain.

[4]U.S. Geological Survey, Fort Collins Science Center, New Mexico Landscapes Field Station, Los Alamos, New Mexico 87544.

[5]Laboratorio Ecotono, INIBIOMA, CONICET-Universidad Nacional del Comahue, Bariloche, 8400 Río Negro, Argentina.

[6]Queensland Herbarium, Environmental Protection Agency, Mt Coot-tha Road, Toowong, Queensland 4066, Australia; School of Biological Sciences, University of Queensland, St Lucia, Queensland 4072, Australia

[7]Autonomous University of Barcelona, Cerdanyola del Vallès 08193, Catalonia, Spain.

Corresponding author: Alistair S. Jump, Biological and Environmental Sciences, University of Stirling, Scotland, FK9 4LA, UK. a.s.jump@stir.ac.uk, +441786467848

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Abstract

Ongoing climate change poses significant threats to plant function and distribution. Increased temperatures and altered precipitation regimes amplify drought frequency and intensity, elevating plant stress and mortality. Large-scale forest mortality events will have far-reaching impacts on carbon and hydrological cycling, biodiversity, and ecosystem services. However, biogeographical theory and global vegetation models poorly represent recent forest die-off patterns. Furthermore, since trees are sessile and long-lived, their responses to climate extremes are substantially dependent on historical factors. We show that periods of favourable climatic and management conditions that facilitate abundant tree growth can lead to structural overshoot of above-ground tree biomass due to a subsequent temporal mismatch between water demand and availability. When environmental favourability declines, increases in water and temperature stress that are protracted, rapid, or both, drive a gradient of tree structural responses that can modify forest self-thinning relationships. Responses ranging from premature leaf senescence and partial canopy dieback to whole-tree mortality reduce canopy leaf area during the stress period, and for a lagged recovery window thereafter. Such temporal mismatches of water requirements from availability can occur at local to regional scales throughout a species geographical range. Since climate change projections predict large future fluctuations in both wet and dry conditions, we expect forests to become increasingly structurally mismatched to water availability and thus over-built during more stressful episodes. By accounting for the historical context of biomass development, our approach can explain previously problematic aspects of large-scale forest mortality, such as why it can occur throughout the range of a species and yet still be locally highly variable, and why some events seem readily attributable to an ongoing drought while others do not. This refined understanding can facilitate better projections of structural

overshoot responses, enabling improved prediction of changes to forest distribution and function from regional to global scales.

Introduction

Changing climate patterns pose significant threats to plant and ecosystem function and species distributions (Kelly & Goulden, 2008). In many areas, increased temperatures and altered precipitation regimes combine to exacerbate drought stress from hotter droughts, significantly elevating plant mortality, from water-limited Mediterranean forests to tropical moist forests (IPCC, 2014; Allen *et al.*, 2015, Greenwood *et al.*, in press). Of particular concern are broad-scale forest die-off events where rapid mortality occurs over 10s to 1000s of km^2 of forest, which could offset any positive tree-growth effects of CO_2 fertilisation and longer growing seasons from warming temperatures during the second half of the 20th Century (Norby & Zak, 2011; Nabuurs *et al.*, 2013; Ruiz-Benito *et al.*, 2014; van der Sleen *et al.*, 2015). Furthermore, widespread forest growth reductions and increases in the extent and magnitude of die-off events are anticipated as climate warms and becomes more extreme and as current climatic extremes become more frequent (Adams *et al.*, 2009; van Oijen *et al.*, 2013; Allen *et al.*, 2015; Frank *et al.*, 2015; Charney *et al.*, 2016; Greenwood *et al.*, in press). Extensive forest die-offs would have far-reaching consequences through impacts on carbon and hydrological cycling, biodiversity, and goods and environmental services to local human populations (Anderegg *et al.*, 2015; Frank *et al.*, 2015; Trumbore *et al.*, 2015).

Ongoing environmental changes are already altering the distribution of species across the globe (Walther *et al.*, 2002; Parmesan, 2006). Contemporary plant range changes have been readily identified in woody species, with range expansions and increases in population density resulting from enhanced growth and reproduction at the upper and poleward edge of species distributions as the climate warms (Sturm *et al.*, 2001; Harsch *et al.*, 2009). Negative changes in plant water balance due to elevated temperature and/or decreased precipitation are expected to locally constrain productivity and elevate mortality (e.g. Juday *et al.*, 2015), with effects being particularly evident at the equatorial and low altitude (or hotter and drier) margins of species distributions (Bigler *et al.*, 2007; Sarris *et al.*, 2007; Allen *et al.*, 2010; Carnicer *et al.*, 2011; Linares & Camarero, 2011; Sánchez-Salguero *et al.*, 2012). Indeed, recent evidence from populations at the equatorial and low altitude range-edge of forest-forming tree species has shown elevated mortality and growth decline linked to rising temperatures and drought stress over the last half-century (Jump *et al.*, 2006; van Mantgem & Stephenson, 2007; Beckage *et al.*, 2008; Piovesan *et al.*, 2008). Drought-linked tree mortality might, therefore, be expected to concentrate along already hotter and drier margins of a species' distribution. However, this is not always the case, with recent drought-linked die-off also occurring throughout species ranges while some range edge populations can be relatively unaffected by regional drought (Jump *et al.*, 2009; Allen et al. 2010; Hampe & Jump, 2011; Allen *et al.*, 2015; Cavin & Jump, 2016). Consequently, simple biogeographical explanations cannot adequately explain the full range of drought-linked tree mortality patterns observed.

Despite the recognised effects of intense droughts and increased temperatures on tree mortality, the die-off patterns observed worldwide are poorly reproduced by global vegetation models (McDowell *et al.*, 2013; Steinkamp & Hickler, 2015). Forests are complex ecosystems, and the responses to climate extremes are dependent on a range of factors including species composition, species-specific plant functional traits (Anderegg *et al.*, 2016a), intraspecific variability, biotic interactions, legacy effects, such as "ecological memory" of past climate, management, or natural disturbances (Johnstone *et al.*, 2016), and stand structure (Fensham *et al.*, 2005; Allen *et al.*, 2015). Another major factor commonly confounding interpretations of the relationships between the drivers and effects of forest dieback is the temporal mismatch between relatively rapid climatic fluctuations in water deficit and temperature and the slower lagged morphological responses of trees. The complexity of the interactions among multiple inciting and exacerbating factors associated with diverse forest mortality processes are highlighted by the varied and divergent patterns and causes attributed to mortality events, even within a particularly well-studied species such as piñon pine (Meddens *et al.*, 2015).

Our knowledge of physiological causes of drought-linked tree mortality has advanced rapidly over recent years as our understanding of the importance of both hydraulic failure and carbon-related aspects, as well as their interaction, has developed (McDowell, 2011; Sevanto *et al.*, 2014; Hartmann *et al.*, 2015; Mencuccini *et al.*, 2015). Likewise, the importance of substrate and biotic interactions, particularly insect pest outbreaks, in exacerbating mortality is well-understood at a general level (Franklin *et al.*, 1987; Anderegg *et al.*, 2015; Fensham *et al.*, 2015; Hartmann *et al.*, 2015; Meddens *et al.*, 2015). However, a strong disparity persists between observed die-off events and our predictive capacity (McDowell *et al.*, 2013). Consequently, there is an urgent need to develop a more integrated approach to understanding broad-scale mortality, incorporating historical and landscape context as well as more immediate environmental drivers (Hartmann *et al.*, 2015).

Here, we consider tree mortality responses to drought, showing that an approach that combines past environmental conditions with current tree structure can improve our understanding of drought-linked mortality events. We begin by considering plant responses to reduced water availability, before looking at the role of stand structure and management in determining response to changes in water availability from a variety of forest ecosystems. We conclude with proposals to improve monitoring and modelling approaches with the aim of improving our predictive capacity of forest dieback across the globe.

Plant-level adjustments to increased water scarcity

Alterations to the availability of resources limiting plant function and growth can be both direct (e.g. water, light and nutrients) or indirect (e.g. through disturbance, pests, pathogens). Plants typically respond to changes in resource availability via the gain or loss of biomass, suggesting that plant biomass should track the recent availability of the limiting resource (Chollet *et al.*, 2014). Commonly, significant time lags in response can occur due to the comparative slowness of plant morphological adjustments (e.g. carbon allocation, Arneth et al., 1998) relative to potentially more rapid changes in resource availability, which could be partially compensated by water storage in plants and soil (Sevanto et al., 2006). However, fluctuations in water availability are of critical importance since the water-storage capacity of most plants is low relative to total daily water demand, even in large trees. This relatively low water-storage capacity renders plants at particularly high risk of structural and functional injury through water deficit on much shorter time scales than through reduction of other resources that can be stored within plant tissues and reallocated (Vaadia *et al.*, 1961; Chapin *et al.*, 1990). Trees generally take advantage of wetter conditions by growing more above-ground biomass (e.g. taller stems and more leaf area), necessary to better compete for light and space when water is abundant. However, when the water limitations of drier climatic conditions inevitably return, this newly developed biomass may become unsustainable and vulnerable to structural dieback. We term this process of increased above-ground biomass development due to more favourable water availability in the past and the consequent temporal mismatch between water availability and demand, *structural overshoot* (SO).

Drought-resistance strategies are varied and range from drought escape (ephemeral species) to drought avoidance (e.g. through efficient stomatal control, drought-deciduousness, increased root:shoot ratio) and drought tolerance (e.g. high resistance to embolism, osmotic adjustment) (Ludlow, 1989; De Micco & Aronne, 2012; Brunner *et al.*, 2015). In perennial species, reducing water loss is a priority under drought (Maseda & Fernández, 2006) regardless of whether it occurs through stomatal closure and/or leaf loss. Stomatal closure has a direct cost in terms of carbon assimilation and may be unsustainable in the long-term (McDowell *et al.*, 2008; McDowell, 2011; Poyatos *et al.*, 2013), whereas structural adjustments (e.g. loss of leaves and above-ground woody tissues) are particularly costly in woody plants. Large woody organs are persistent and cannot be discarded during periods of water scarcity without partial or total mortality. Similarly, at the stand level, water availability per individual will depend on the overall water demands of the plants competing for the same water resources. Measures of stand structural development, such as stem density, basal area, or leaf area index (LAI), relative to a long-term baseline, should then be significant contributing factors to the drought susceptibility of forest stands through structural overshoot under fluctuating climate conditions (Ruiz-Benito *et al.*, 2013).

Stem density and leaf area influence on tree responses to extreme droughts

According to the above rationale, drought-induced tree mortality should be more pronounced where stem density is the highest, all else being equal. We explored the validity of this hypothesis relative to drought-linked tree mortality across biomes by performing a review of the scientific literature using search terms “drought” and “mortality” and including quantitative, field-based observational research studies performed on adult trees (see Appendix S1 for full details). Of the 75 papers that identified drought-induced tree mortality (DITM), tree density was the most commonly mentioned covariate in DITM events (33% of cases) alongside biotic agents (i.e. insects, pathogens or herbivores, 29% cases) (Fig. 1). While the overall risk of drought-induced forest mortality is consistent across biomes (Greenwood *et al.*, in press), density and biotic agents as co-drivers of DITM were more often reported in more water- or temperature-limited systems such as tropical savanna and temperate forests, respectively (Fig. 1). Tree mortality in tropical systems overall was more frequently related to the sole effects of episodic droughts or drought in combination with fire (Fig. 1). However, the lower frequency of drought when compared to fire may be influenced by the focus and methods of studies in tropical biomes (i.e. generally focussed less on density effects and biotic agents). Overall, we found that 71% of the 28 cases testing density effects reported a positive association between density and mortality (i.e. higher mortality in denser stands), 14% did not report a significant effect, and 14% reported higher mortality in less dense stands. A single study reported mixed positive and negative density dependent effects. Furthermore, the sign of the density effect was relatively independent of the forest type (Fig. 2).

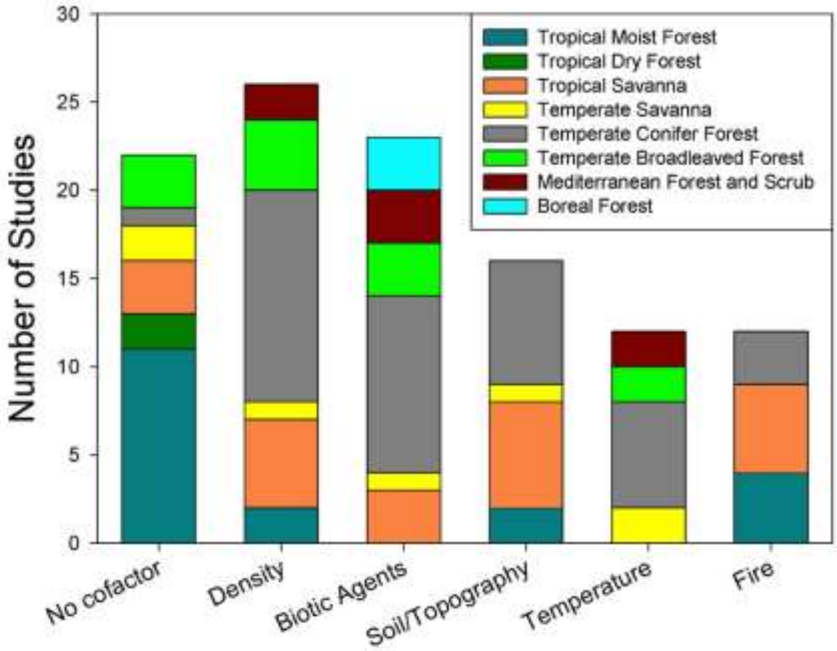

Figure 1. Quantitative, field-based observational studies of drought-induced tree mortality that identify as drivers of drought alone (i.e. no cofactor) and co-drivers that interacted with drought in forest types classified following Olson *et al.* (2001) biomes.

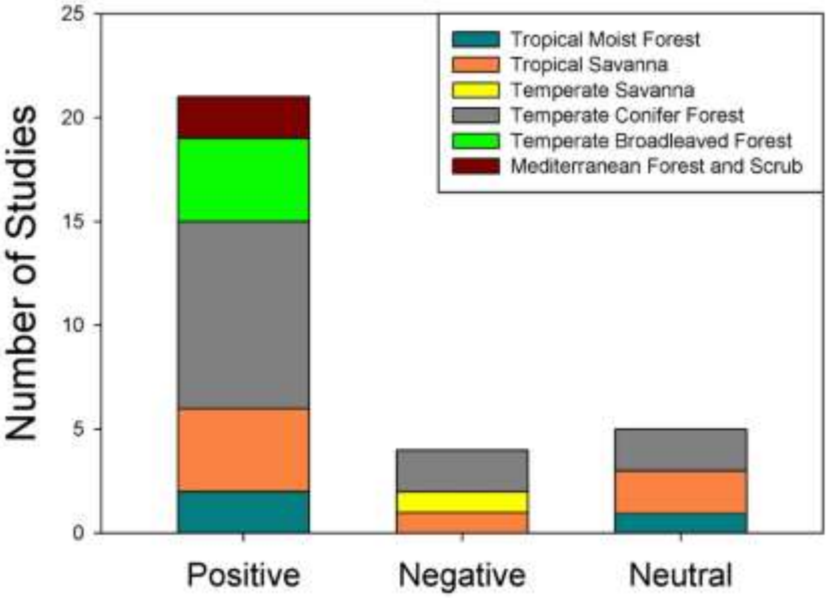

Figure 2. Frequency of positive, negative or neutral effect of stand density on drought-induced tree mortality among quantitative, field-based observational studies in forest types classified using Olson *et al.* (2001) biomes.

While stand density is generally a co-driver in drought-induced tree mortality, total leaf area is a major determinant of plant water requirements and, therefore, has the potential to mediate drought impacts from individual organs up through the whole-forest scale (Fig. 3). Stand-level leaf area is normally expressed as the leaf area index (LAI), corresponding to projected canopy leaf area relative to ground area (m^2 m^{-2}), which can be calculated as the product of the projected leaf area of each tree (hereafter, crown leaf area, m^2 $tree^{-1}$) and stand density (tree m^{-2}). LAI can be used as a proxy of functional responses to resource availability, as for example with water availability (Margolis *et al.*, 1995; Pook *et al.*, 1997; Smettem *et al.*, 2013; Duursma *et al.*, 2016), and combines a number of ecosystem properties that are dependent on climate, forest management, and legacy effects (Johnstone *et al.*, 2016). Furthermore, LAI is dynamic and changes with stand development and self-thinning processes (Holdaway *et al.*, 2008) and is critical in driving forest productivity (Reich, 2012). LAI also depends on forest type and climate, where temperature limitations on LAI have been identified in cool climates whereas water availability is the main climatic driver in other climates (Iio *et al.*, 2014), with LAI decreasing as water stress increases (Grier & Running, 1977; Luo *et al.*, 2004). Since LAI is coupled to the temporal availability of water, including pulsed deficits as drought (Iio *et al.*, 2014), drought is expected to lead to LAI and biomass reductions along a gradient of response running from premature leaf senescence and partial canopy dieback, to whole plant mortality (Fig. 3) such that drought-induced tree dieback and mortality events result from the temporal mismatch between LAI and water availability in a given environment.

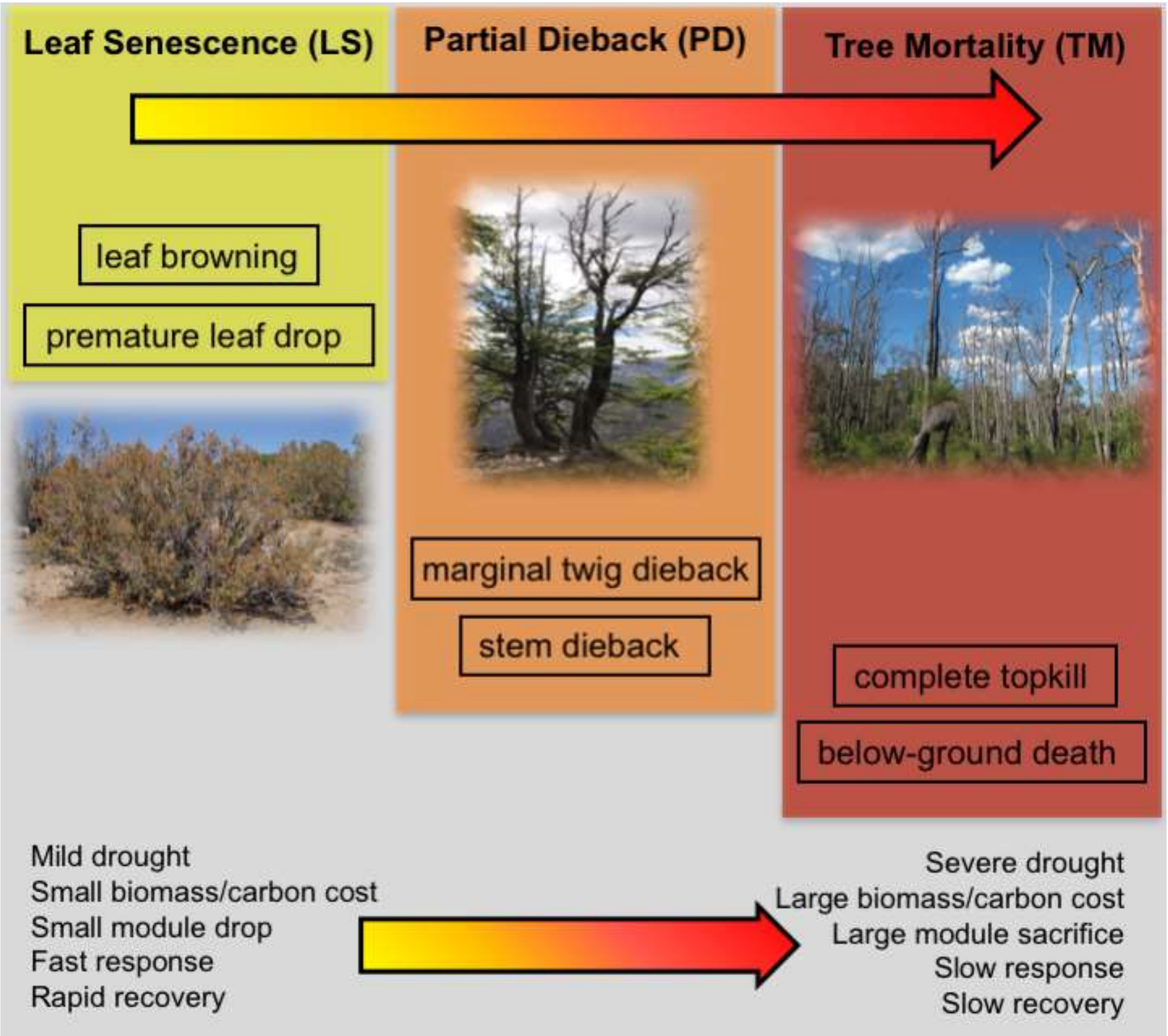

Figure 3. Spectrum of tree or forest structural loss responses to decreases in water availability, or increases in drought stress. Photographs: Extensive premature leaf senescence (LS) of one-seed juniper (*Juniperus monosperma*), northern New Mexico, USA (2013, C.D. Allen), in response to protracted and extreme hotter drought (Allen *et al.*, 2015). Partial dieback (PD) of canopies of evergreen coihue (*Nothofagus dombeyi*), Patagonia, Argentina (2015, T. Kitzberger), from both extreme and chronic drought (Suarez & Kitzberger, 2010). Complete topkill tree mortality (TM) of jarrah (*Eucalyptus marginata*), southern Western Australia (2012, C.D. Allen), triggered by extreme hotter drought in early 2011 and a chronically drying climate (Matusick *et al.*, 2013).

Leaf area index under changing resource availability

Resource limitations are at the base of our understanding of tree growth and forest dynamics. To the extent that forest resource use is determined by the product of tree density and individual tree size, both variables cannot increase at the same time (unless resources are not limiting). This is at the core of self-thinning theory, which predicts a negative relationship between tree density and tree size during forest development over time, at least within a range of tree densities and for even-aged stands (Yoda *et al.*, 1963). This negative relationship is normally described using a power law (linear in log-log scale) independently of the tree size measure used (Westoby *et al.*, 1984; Weller, 1987; Zeide, 1987). Several variables have been used to describe tree size (e.g. biomass, diameter, height, crown size), resulting in different self-thinning slopes. Here, we propose the use of crown leaf area as a measure of tree size when studying resource limitations in the context of drought-induced responses (see Fig. 4), since variables related to crown leaf area are arguably good proxies for individual resource use and physiological responses to specific perturbations, particularly drought. Furthermore, its relationship with crown allometry and growing-space-filling, instead of diameter or biomass, make the corresponding relationship between stem density and crown leaf area highly interpretable for individual and species-specific responses (Morris, 2003; Pretzsch & Schütze, 2005; Charru *et al.*, 2012). For simplicity, we assume that the slope of the log relationship between crown leaf area and tree density is -1, implying constant LAI over time at the stand level (unless resource availability changes), as is traditionally assumed during self-thinning (Long & Smith, 1984; Osawa & Allen, 1993; but see Holdaway *et al.*, 2008; Coomes *et al.*, 2012). However, our application of the proposed framework to forest SO responses to drought does not depend on this particular assumption and would apply regardless of the slope of the relationship as long as it is negative (Coomes *et al.*, 2012).

The generality of the ideas underlying the self-thinning line (STL) concept makes it a powerful model to understand the impact of changes in resource availability on forest structure since its intercept is frequently dependent on resource availability (sometimes treated as site quality, Appendix S2). Modifications of the STL have been widely studied across different sites and species, whereas studies covering variations over time are scarcer (Appendix S2). The STL intercept increases with higher resource availability or productivity for a given species or, more generally, with release from any previously limiting factor (Bi, 2001; Weiskittel *et al.*, 2009; Zhang *et al.*, 2013; and Appendix S2). The slope of the STL relationship can be modified by differences in shade-tolerance (Pretzsch & Biber, 2005; Weiskittel *et al.*, 2009), perturbations (Oliver, 1995; Coomes *et al.*, 2012) and changes in soil fertility (Morris, 2003) and due to inter-site variability (see a complete description in Appendix S2). However, generally, the slope of the STL varies little through time (Pretzsch *et al.*, 2014) and space (Bi *et al.*, 2000; Bégin *et al.*, 2001; Bi, 2001), at least when there is no recruitment limitation and mature forests are experiencing competitive thinning (Duncanson *et al.*, 2015). Furthermore, although lower slopes could occur under increased aridity, intercept variations are much stronger than slope variations (Deng *et al.*, 2006; Dai *et al.*, 2009; Bai *et al.*, 2010). Consequently, we base our conceptual framework of drought responses on the expectation that changes in environmental conditions over time should result in a range of approximately parallel relationship between crown leaf area and tree density within a site (Fig. 4a; and references in Appendix S2), as it is generally supported by changes through time (Garcia, 2012; Pretzsch *et al.*, 2014). We note, however, that the general principles presented here would still apply if alternative ‘self-thinning lines’ were not strictly parallel.

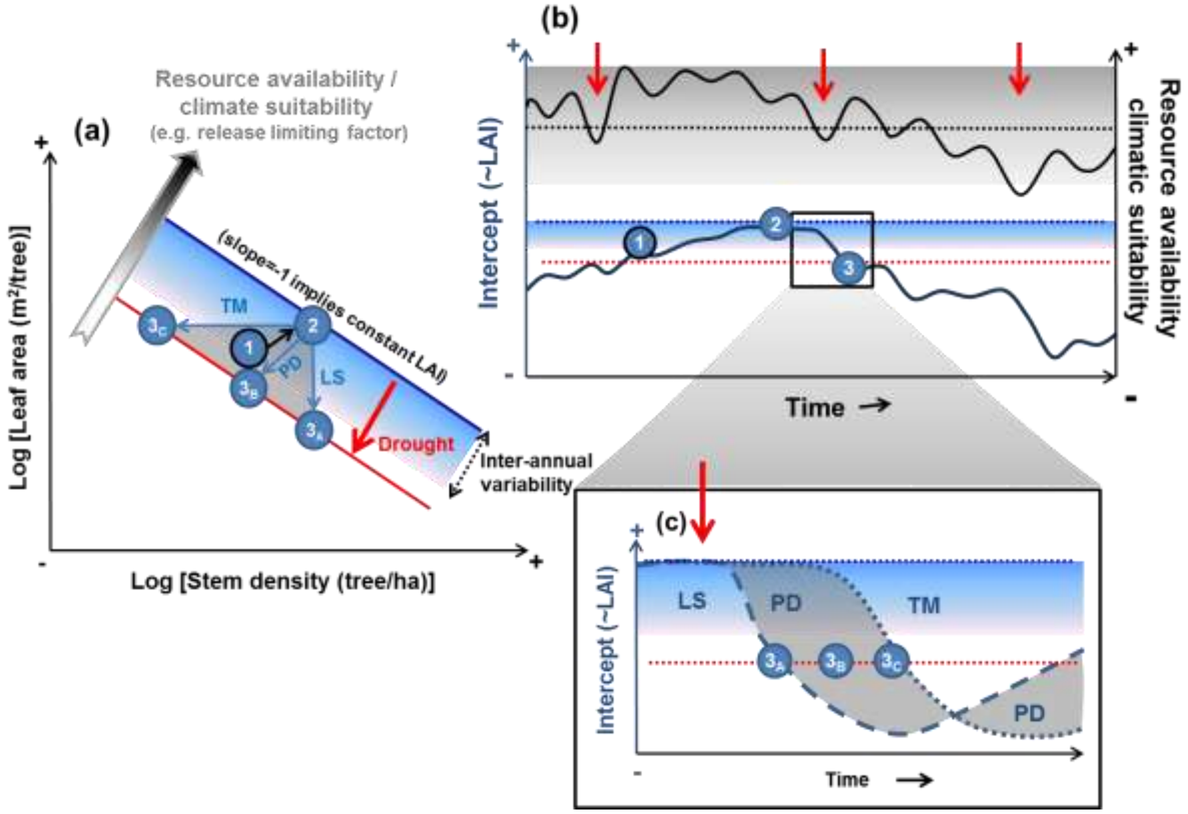

Figure 4. Structural overshoot (SO) framework highlighting temporal mismatches between resource demand and supply. Resource demand is assumed to be proportional to leaf area index (LAI) in a concept analogous to self-thinning but using crown leaf area as a measure of individual tree size. Panel **(a)** shows the theoretical effect of an extreme drought (red arrow) on the ‘self-thinning’ intercept (i.e. when stem density=1 tree ha^{-1}), equivalent to the leaf area index (LAI) of the stand. The situation depicted in the figure illustrates a forest stand located initially in a position (state 1) from which there is an increase in LAI and stand density over time (to state 2) due to release from a limiting factor. Under an extreme drought event, there is a reduction in stand-level LAI, that can occur through: leaf senescence (LS) only, state 3_A;

diverse combinations of partial dieback (PD) affecting canopy branches and whole stems (in multi-stemmed species), state 3_B (shown as a grey zone); or individual tree mortality (TM), state 3_C. Panel **(b)** shows the temporal dynamics of resource availability/climate suitability (upper graph, dotted black line represents average climatic conditions) and the associated changes in the intercept of the self-thinning line (LAI) (lower graph, including the dotted blue and red lines, which show the intercept for the continuous blue and red lines in panel (a), respectively). We highlighted the impact of three severe droughts using red arrows: the first drought event occurs when forest LAI is still relatively low, and hence the impact on the stand is minor; the second drought occurs when LAI is higher and, therefore, the corresponding response in terms of LAI reduction is also larger (a detailed response is depicted in panel (c)); and, the third arrow depicts an hypothetical situation in which forest resilience has been lost due to continuously worsening conditions and thus an additional drought may result in extreme LAI reductions (not depicted in panels (a) or (c)). The location of the states (1) (i.e. initial state), state (2) (i.e. when self-thinning is occurring under high resource availability and/or climatic suitability), and state (3) (i.e. potential state under persistent severe droughts exceeding the inter-annual variability and potentially leading to new self-thinning lines) are also shown. Panel **(c)** shows a more detailed temporal response of the self-thinning intercept to a drought event, illustrating different dynamics depending on whether the response is primarily through leaf senescence (LS), partial dieback of canopy branches and stems (PD, grey zone), or extensive tree mortality (TM).

Temporal mismatch between water demand and availability drives the spectrum of tree dieback responses to drought.

Following a period with increasing resource availability (or release from previous limiting factors, such as conditions following disturbances), the self-thinning line would move away from the origin (higher intercept), which implies higher LAI (and water use) at the stand level (Fig. 4a,b). There is increasing evidence that leaf area at both the tree and stand levels responds to changes in water availability, but frequently with lagged responses (Bigler *et al.*, 2007). These lags arise from the fact that the water status of trees can be buffered from seasonal or even longer-term variations in climatic water availability (due to, e.g. deep rooting) and also from the fact that individual trees have a substantial capacity to accommodate short-term changes in water stress even without leaf loss (Martínez-Vilalta *et al.*, 2014). As a result, temporal changes in LAI are frequently smaller than those observed when comparing the mean conditions of different sites along analogous gradients in water availability (Smettem *et al.*, 2013). A frequent consequence of LAI dynamics lagging somewhat behind environmental changes is the temporal mismatch of resource availability and LAI; in particular, when severe stress occurs after a strongly favourable period, the large difference between resource demand (determined by lagged LAI) and resource availability results in a forest structurally maladapted to the current stressful conditions. We hypothesise that the potential for SO dieback dynamics to occur depends upon the particular magnitude, timing, and sequence of climatic fluctuations, which drive the size and duration of the temporal mismatch between legacy LAI levels and resource availability.

Given that temporal variability in water (or other limiting resources) drives the development of high tree LAI relative to subsequent resource availability, the resulting SO eventually leads to dieback reductions in leaf area. Individual tree responses can be put in a wider context of diverse structural plant adjustments (Fig. 3), ranging from premature leaf senescence (LS) to partial dieback (PD) of canopies and stems to complete tree mortality (TM). We expect that LAI adjustments will occur more rapidly if they occur through leaf senescence, resulting in shorter temporal lags between water availability and demand. At the other extreme, a response through tree mortality, with a much larger cost in terms of biomass, would tend to occur more slowly and result in longer lags (Fig. 4c), although outbreak dynamics of mortality-causing biotic agents such as bark beetles can drive relatively rapid tree mortality (Anderegg et al. 2015). The implications in terms of recovery at tree and stand levels after disturbance are substantial. Recovery after LS occurs primarily through the growth of new foliage once environmental conditions return to a relatively favourable state, which requires the consumption of stored carbohydrates (Galiano *et al.*, 2011). Recovery from PD, if developmentally possible for the species, additionally requires some level of woody tissue resprouting from the crown, stem, or roots, with an associated greater cost to stored carbohydrate resources, implying slower response times (Galiano *et al.*, 2012). Finally, recovery after complete TM depends on new recruitment, implying even longer response times (Fig. 4c). The response spectrum between LS and TM can be seen as a continuum – they may occur simultaneously in co-occurring species or in different trees of a given population, in which more severe levels of resource stress (or disturbance) increase the likelihood of a TM response (Fig. 3). These three types of responses often occur sequentially in time, starting with LS, followed by PD and, if the stress is intense or persistent enough, resulting in TM (e.g. Galiano *et al.*, 2011). However, they also seem to be site- and species-dependent to varying degrees, as we illustrate below.

Structural overshoot and the spectrum of drought-induced forest dieback around the world

Different tree species show different strategies in their response to chronic and acute drought stress linked to differences in traits, population history, and the temporal patterns of drought occurrence to which they are adapted. Consequently, changes in water availability can result in a variety of responses at the population level such that seemingly disparate responses in different systems are linked through the SO concept along a continuum, from leaf drop to whole plant mortality (Fig. 3). The origin of structural overshoot is usually due to the existence of favourable conditions for growth (e.g. wet or drought-free periods) together with certain management actions or omissions that favour tree encroachment (Table 1). On the one hand, historical climatic variability promotes favourable conditions for growth and biomass increments generally at centennial or decadal periods: centennial such as in *Eucalyptus*-dominated savannah from NE Australia (Fensham *et al.*, 2005; Fensham *et al.*, 2012), multi-decadal for conifer forests of SW North America (Williams *et al.*, 2013; Allen *et al.*, 2015; Williams *et al.*, 2015), or decadal such as in austral *Nothofagus* forests in South America (Suarez *et al.*, 2004; Suarez & Kitzberger, 2008; Suarez & Kitzberger, 2010). On the other hand, human legacies have coupled with climatic variation through successional vegetation growth since the last disturbance or exploitation, ranging from settlement fires in Andean Patagonia, and agricultural and timber exploitation cessation in Europe, to logging in tropical forests or ranching in SW North America and Australia (Table 1, Fig. 5). The accumulation of biomass may be further promoted with forest fire protection (as in South American *Nothofagus* forests), increasing stand densities as well as fuel accumulation and the risk of future fires (as in North American *Pinus* forests, Table 1).

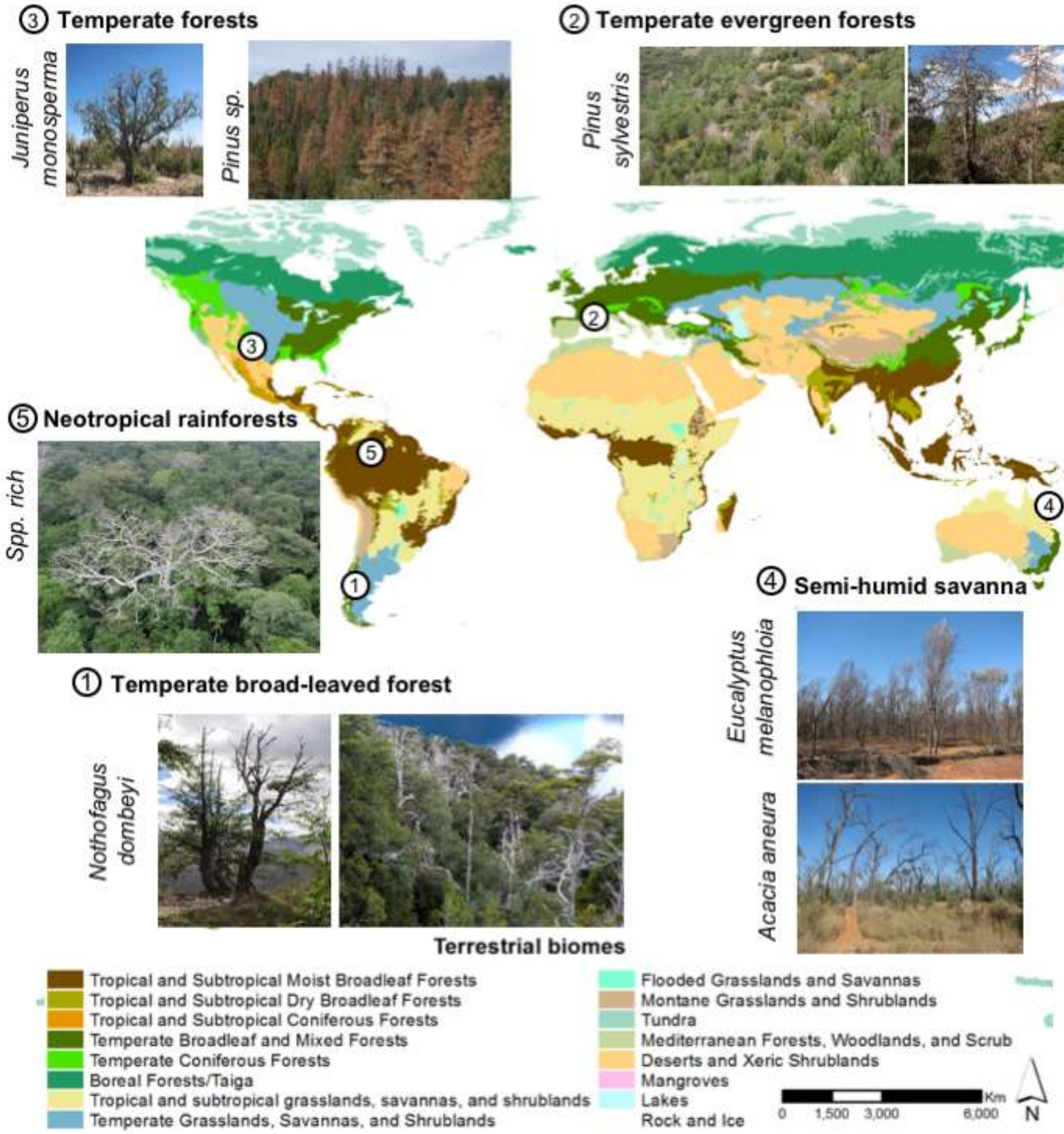

Figure 5. Map location and illustrations of structural overshoot (SO) responses of the case studies summarised in Table 1 and Appendix S3, overlaid on major terrestrial biomes modified from Olson *et al.* (2001). (1): tree mortality of *Nothofagus dombeyi* near Bariloche (Argentina) (photo T. Kitzberger and F. Lloret); (2): tree mortality of *Pinus sylvestris* in Prades (Tarragona, Spain) (photo R. Martin Vidal) and in Teruel (Spain) (F. Lloret); (3): partial dieback of *Juniperus monosperma* in New Mexico (USA) and tree mortality of *Pinus* sp. in Sequoia Natural Park (USA) (photo C. D. Allen); (4): tree mortality of *Eucalyptus*

melaniploia sp. and *Acacia aneura* in Queensland (Australia) (photo R. Fenshman); (5): tree mortality in species rich forests in western Amazonian (Brazil) (photo NASA/JPL-Caltech from Saatchi *et al.* (2013)).

After periods of biomass accumulation due to both climatic variability and legacy effects, extreme drought events might easily result in SO in a wide variety of forest and tree species (Table 1). Extreme drought may also occur in the context of multiyear climatic oscillations, such as ENSO leading to peaks of drought in the wet season of South American *Nothofagus* forests or extremely low rainfall in the dry season in Amazonian tropical rainforests (see references Table 1). The effects of multiyear droughts can accumulate during several years and eventually result in temporal peaks of extensive mortality (e.g. NE Spain, SW North America and Queensland). Drought effects are commonly reinforced by abiotic and biotic co-drivers, as high temperatures (e.g. SW Argentina, NE Spain, SW North America), soils with low water holding capacity (e.g. S and NE Spain and Queensland), antagonistic biotic interactions (fungal diseases, plant parasites such as mistletoe, insect outbreaks (e.g. NE Spain, SW North America), wildfires (e.g. SW North America and Amazonia), logging and/or habitat disruption (e.g. Amazonia) (Table 1). Some of these co-drivers, in turn may be reinforced by the loss of vigour that usually accompanies SO and tree mortality, such as in the case of biotic antagonists (Franklin *et al.*, 1987), or by the resulting transformation of the environment (Allen, 2007).

The variety of tree-level responses, from LS to PD and individual TM, seems to obey on the one hand the intensity and frequency of droughts (Figure 3) and on the other hand the anatomical and structural differences between species. For example, PD seems to be particularly common in *Fagaceae* and *Nothofagaceae* (Suarez *et al.*, 2004; Galiano *et al.*, 2012), while *Pinaceae* show a more continuous pattern of LS until eventual TM (Galiano *et al.*, 2010; Galiano *et al.*, 2011; Poyatos *et al.*, 2013). Leaf area reductions predicted by the SO framework can eventually translate to changes in the dominant species, particularly when TM is the more conspicuous response (e.g. Allen and Breshears, 1998). Considering the dominant structural responses of the forests (Table 1) while species self-replacement may occur in some cases (Hosking & Hutcheson, 1988), shifts, when they occur, tend to favour more drought-tolerant species, for example, *Austrocedrus chilensis* in *Nothofagus dombeyi* forests (Suarez & Kitzberger, 2008), and *Quercus ilex* or *Q. pubescens* in *Pinus sylvestris* forests (Galiano *et al.*, 2010; Rigling *et al.*, 2013). When the phenomenon extends over large areas, such in SW North America, vegetation shifts can be strongly evident at ecotones (Allen & Breshears, 1998). However, we do not have enough information to identify clear, general trends of species replacement and vegetation shifts, substantially because of large uncertainties in the mid-term fate of the regeneration of the different species (Martínez-Vilalta & Lloret, 2016). At the ecosystem level, tree mortality events have led to an important loss of forest area and stored carbon (Table 1). The reduction of live standing biomass by mortality can in turn increase dead fuel loads, thereby increasing fire risk rapidly (e.g. *Nothofagus* in SW Argentina and tropical rainforest).

Table 1. Summary of five diverse case studies illustrating the SO framework Summary of structural overshoot examples from five continents, including SO legacy causes (both climatic and management legacies), SO response drivers (i.e. climatic drivers and other co-drivers), affected stand conditions and landscape settings, and predominant structural responses. The main affected tree species of each case study are (1): *Nothofagus dombeyi*; (2): *Pinus sylvestris, Quercus ilex*; (3): *Abies* spp., *Pseudotsuga menziesii*, *Populus* spp., *Pinus ponderosa*, *Quercus* spp., *Pinus edulis*, and *Juniperus monosperma*; (4): *Eucalyptus* spp. and *Acacia* spp.; and (5): species-rich forest. See Appendix S3 for additional text description of each case study.

Case study (region)	**SO legacy cause**		**SO response drivers**		**Affected conditions** (stand level, functional group, biogeographical location)	**Predominant structural responses**
	Climatic legacy	**Management legacy**	**Climatic driver**	**Other co-drivers**		
1. Temperate broadleaved forest (N Patagonia, SW Argentina)	Wet or drought-free growth periods	Fire suppression after settlement	Extreme droughts in the wet season; failure of deep soil water recharge	Summer temperatures	High density stands. Trees with declining growth. Dry edge of species range	Massive partial dieback, tree mortality
2. Temperate evergreen forest (Spain)	Wet or drought-free growth periods	Agricultural and timber exploitation abandonment	Extreme droughts over the baseline trend	Shallow and stony soils, mistletoe, fungal pathogens	High density stands. Dry edge of species range	Premature leaf senescence, delayed tree mortality

3.Temperate forests (SW USA)	Wet or drought-free growth periods	Fire exclusion due to ranching and suppression	Episodic extreme droughts, increasing background drought stress	Temperature, insect outbreaks, fungal diseases, amplified fire	High-density stands and some low density. Trees with declining growth. Large and tall trees. Dry edge of species range	From premature leaf senescence and partial dieback to extensive tree mortality
4. Sub-humid savanna (Queensland, Australia)	Biomass load growth during wet periods of the 1950s and 1970s	Difficult to discern	Intense multiyear droughts	Geology, soils	High density stands. Fast growing dominant species, tall trees, high shoot to root. Core of species range	Massive tree mortality
5. Neotropical rainforests (Amazonia & Central America**)**	Increased biomass growth during drought-free periods	Increased recruitment when canopies are opened by logging	ENSO-related droughts and low dry season rainfall	Fire, logging, fragmentation	Fast growing dominant trees, tall emergent trees, species with low wood density, non-sprouters	Premature leaf senescence, branch dieback, pulses of tree mortality.

Key references used in the case studies **(1)**: Suarez *et al.* (2004), Suarez & Kitzberger (2008, 2010); **(2)**: Galiano *et al.* (2010), Hereş *et al.* (2012), Vilá-Cabrera *et al.* (2013), Aguadé *et al.* (2015); **(3)**: Gitlin *et al.* (2006), Williams *et al.* (2013), Griffin & Anchukaitis (2014), Anderegg *et al.* (2015), Meddens *et al.* (2015), Allen (2016); **(4)**: Fensham & Holman (1999), Fensham *et al.* (2005, 2010), Dwyer *et al.* (2010); and **(5)**: Condit *et al.* (1995), Chazdon *et al.* (2005), Rolim *et al.* (2005), Nepstad *et al.* (2007), Costa *et al.* (2010), Saatchi *et al.* (2013).

Implications for forest prediction, monitoring and management under environmental change

The structural overshoot framework is based upon a straightforward premise: that in plant water economy, resource demand cannot outstrip resource supply for an extended period. When such temporal mismatch occurs, the result is a spectrum of tree dieback and mortality (Fig. 3). The generality of the framework is emphasised by its applicability from tree to forest scales. At the whole-tree scale, tree mortality represents the most extreme response that reduces water demand below the available water supply, resulting in landscape-scale declines in demand through widespread reduction in tree density –analogous to self-thinning at the forest scale (Fig. 4).

Given that current rising mean temperatures are projected to be accompanied by increases in the frequency, magnitude and duration of extreme climatic events, forests across the globe will be exposed episodically to greater drought stress (Adams *et al.*, 2009; Allen *et al.*, 2010; Williams et al. 2015; Allen *et al.*, 2015; Frank *et al.*, 2015). An important implication of projected increases in climatic variability in many regions of the world (IPCC, 2014) is that increased fluctuations in water availability may amplify the degree of structural overshoot. As a consequence, large areas of forest may become at risk of dieback effects, even in cases in which LAI remains approximately constant over time. SO may also be exacerbated by transient increases in productivity due to fertilization effects (CO_2, nitrogen), which likely will contribute to divergences between current and sustainable LAI. Indeed, already-witnessed mortality events are not limited to the hotter and drier margins of species distributions (e.g. Fensham *et al.*, 2015) because tree biomass and/or leaf area is expected to adjust to the maximum supportable by the available resources in any given area (Bonan

2002). More variable, hotter drought may then result in water availability becoming either a chronic or acute limiting factor for growth, even in regions of a species' distribution where this was not previously the case (Chapin *et al.*, 1987). Consequently, any reduction in the availability of this critical resource can induce a parallel reduction in live biomass, and specifically in LAI. The SO framework, therefore, provides a clear rationale for why forest mortality episodes are spatially variable and can be sudden – since the mechanism for SO is derived from thresholds of water resource demand and availability (Fig. 4). While the framework allows for a clear qualitative understanding of expected forest-drought responses, additional data are required to move to quantitative predictions of spatiotemporal vulnerability, as we outline below.

Our SO framework is based on several assumptions. Firstl, we assume that competition for resources is an important determinant of forest demography, ultimately determined by the balance between resource supply and demand. There is overwhelming evidence showing that stand structure, including land-use and management legacies, is a key driver of forest demography (Vilá-Cabrera *et al.*, 2011; Canham, 2014). Second, leaf area index (LAI) and crown leaf area are good proxies for water demand and, therefore, respond to soil water availability and atmospheric water demand (Grier & Running, 1977; Eagleson, 1982; Margolis *et al.*, 1995), with LAI dynamics frequently lagging behind fluctuations in water availability over time (Gholz, 1982; Nemani & Running, 1989; Hoff & Rambal, 2003). Finally, a corollary of the previous points is that temporal mismatches between LAI and water availability (periods in which current LAI is higher than the long-term sustainable value) are associated with increased dieback risk. Although some temporal variation in LAI due to water availability is well-supported by evidence (as we discuss above), to validate our framework the increased dieback risk needs to be empirically tested. This hypothesis can be addressed experimentally by locally modifying the water balance and monitoring the stand-level responses in terms of LAI and tree mortality for a long-enough period of time (e.g. Martin-StPaul *et al.*, 2013). In addition, long-term time series of LAI dynamics from remote sensing may relate increases in LAI to mortality or dieback risk (Van Gunst *et al.*, 2016).

To realize the predictive potential of our framework, we need to better understand the dynamics and determine locally relevant thresholds of LAI (e.g. Osem & O'Hara, 2016). Most vegetation models use spatially-explicit estimates of LAI as a key input that determines canopy processes and, indirectly, the water balance (e.g. Running & Coughlan, 1988; Cáceres *et al.*, 2015) and some account for feedbacks on LAI dynamics (e.g. Landsberg & Waring, 1997). However, inadequate knowledge of LAI drivers and dynamics (including the specific process drivers of premature leaf drop) currently constrains the ability of vegetation models to realistically simulate temporal mismatches between LAI and water availability with sufficient (at least annual) temporal resolution. New developments in remote sensing of LAI (cf. Zheng & Moskal, 2009) will provide opportunities to better link observed spatial and temporal changes in landscape-scale LAI with time-series data of climate drivers (e.g., precipitation and temperature), thereby supporting development and parameterization of improved empirical and mechanistic models relating changes in LAI with temporal variation in the local water balance, particularly including temporal mismatches and lags (cf. Young et al. 2017). A potential mismatch between LAI values predicted from these models with equilibrium estimates of maximum LAI predicted under different climate scenarios would then enable us to assess the potential for dieback at the stand scale.

While the potential for our approach to improve spatial predictions of decline risk appears reasonably straightforward, it currently seems difficult to predict the timing of SO responses, as this depends on our ability to precisely quantify LAI thresholds. In any case, the SO framework provides an operative means of complementing studies assessing forest vulnerability from species-level traits (e.g. Anderegg *et al.*, 2016a) by allowing spatially explicit risk assessments within species ranges (cf. Bradford and Bell 2017). Although physiological safety margins should, in principle, provide the best vulnerability estimates (e.g. hydraulic safety margins, Choat *et al.*, 2012; Anderegg *et al.*, 2015), currently we are very far from being able to determine this information at relevant spatial scales and resolutions.

Nonetheless, it is increasingly being recognised that to adequately determine the status, trends, and magnitude of changes in forests worldwide, there is an urgent need to develop adequate techniques to detect and assess drivers of forest stress and mortality at broad spatial scales (e.g. global forest monitoring, Allen *et al.*, 2010; McDowell *et al.*, 2015; Trumbore *et al.*, 2015). Effective monitoring requires continental and global acquisition of data on tree condition and biomass allocation. Furthermore, such data should be available at an appropriate spatial resolution and intervals short enough to allow detection of the full range of forest dieback responses from premature leaf senescence to whole-tree mortality. Given this combined challenge of scale, resolution and frequency of observation, remote sensing must play the major role in such assessments (Jump *et al.*, 2010). Increased capabilities for high-resolution mapping and monitoring through time of forest dieback and tree mortality events at landscape and regional scales are emerging rapidly (Hansen *et al.*, 2013; Mascaro *et al.*, 2014; Asner *et al.*, 2016; Cohen *et al.*, 2016; Franklin *et al.*, 2016; Mildrexler *et al.*, 2016; Schwantes *et al.*, 2016). Similarly, recent progress in the capabilities for monitoring forest structural characteristics (e.g. Crowther *et al.*, 2015; Zhang *et al.*, 2015; Asner *et al.*, 2016) now provide potential opportunities to better identify current forest vulnerabilities to the spectrum of SO responses to climate variability and change. These new methods offer opportunities to better assess and attribute the processes and drivers of particular forest dieback episodes, which would then provide valuable inputs for empirical models of tree mortality vulnerability at varying spatial resolutions (e.g. De Keersmaecker *et al.*, 2015; Mitchell *et al.*, 2016).

However, despite the rapid development of remote-sensing products to provide greater spatial resolution, data availability remains problematic owing to the high cost of many products when applied over large areas. Furthermore, we must be able to better estimate LAI and determine LAI dynamics, and to differentiate between different patterns of individual biomass allocation (Zheng & Moskal, 2009). Remotely-sensed data collected over broad spatial scales are generally of too coarse a resolution to allow an understanding of how leaf area of the system is partitioned at the individual, population and community level or what post-drought changes in LAI mean - for example, leaf flushing, epicormic sprouting, or the re-establishment of the same or different species. In principle, fine resolution synthetic aperture radar (SAR) and LIDAR can allow effective monitoring of forest structure, however, the challenge of collecting and analysing such data at an appropriate assessment interval and spatial scale remains.

Remote sensing must be paired with effective ground-based monitoring through integration of existing national forest inventory data with global monitoring efforts, such as ICP forests. Moreover, plot-level monitoring must be developed to consistently allow assessment of management impacts and tree allometric relationships, together with reporting of premature leaf senescence and partial dieback. Such data would allow us to better forecast changes in forest structure and function related to human intervention, as well as more effectively calibrate remote sensing methods and better interpret the data that result (Jump *et al.*, 2010). Practically, however, ground-based plot-level monitoring will be limited by observation frequency given the intensive effort required for their collection. Nonetheless, the challenges associated with quantity of data needed at appropriate scale, resolution and monitoring interval can be overcome. First, we must develop a better understanding of the spatiotemporal dynamics of LAI and the relative importance of rainfall deficit, increased temperatures and their combination in driving mortality. Less frequent and less intensive monitoring could then be paired with targeted and responsive frequent and high-resolution monitoring of 'at risk' areas determined based on this improved understanding of SO drivers.

A corollary of the scope for improved forest monitoring is that without such efforts, the occurrence of SO also can complicate determination of the proximate causes of any particular observed pattern of tree structural dieback responses, since the same pattern of risk can be arrived at via differing routes. Lack of adequate monitoring data can, therefore, make it difficult to differentiate the contribution of historical factors (i.e. development of high total canopy leaf area during a preceding wet period) from the main proximate driver of resource stress (e.g. dry moisture conditions). This issue is in addition to the general challenges of interpreting the diverse array of patterns and processes associated with drought-related forest dieback episodes, which emerge from the interactions among a variety of additional tree stressors, in concert with numerous compensatory factors that reduce vulnerability (e.g. Lloret *et al.*, 2012; Allen *et al.*, 2015; Martínez-Vilalta & Lloret, 2016).

Where monitoring and/or model projections identify forests as vulnerable to the SO spectrum of dieback responses to anticipated climate variability or climate change, management actions can be considered in order to lessen the risk and magnitude of dieback and mortality

(Millar *et al.*, 2007; Keenan & Nitschke, 2016). Potential forest management actions to moderate SO include treatments to directly reduce canopy leaf area, tree density, basal area, or even mean tree height by means of mechanical treatments like pre-commercial thinning or commercial timber harvest (D'Amato *et al.*, 2013; Elkin *et al.*, 2015; Giuggiola *et al.*, 2015; Sohn *et al.*, 2016; Bottero et al. 2017; Bradford and Bell 2017). Clearly, SO management should account for the specific benefits (i.e. wood production, catchment water supply, etc.) obtained for a particular forest by paying special attention to LAI changes coupled with climate fluctuations. The addition of prescribed fire to mechanical thinning treatments can sometimes be used to reduce SO stresses (Tarancón *et al.*, 2014). It is interesting to note that frequent-fire-adapted forests can become over-built in ways analogous to SO through human fire suppression, which can increase the risk of high-severity fire in these forests (Enright *et al.*, 2015; Allen 2016). In these cases, combinations of mechanical thinning and burning treatments can also increase the persistence and long-term carbon storage of such forests by lowering risks of stand-replacing fires (Allen *et al.*, 2002; Hurteau *et al.*, 2016).

It is essential to recognise, however, that thinning by mechanical or fire means is not desirable or appropriate in many forest settings for diverse reasons, including ecological, ethical, aesthetic, economic, scientific, conservation, or logistical considerations (McDowell & Allen, 2015). Other management options to lessen forest vulnerabilities to SO-induced dieback range from actions to maintain more water on-site (Grant *et al.*, 2013; Sun & Vose, 2016) to possibly modifying the genetic and/or tree species composition of forest stands toward more drought-resistant genotypes or species (e.g. Aitken & Whitlock, 2014; Fares *et al.*, 2015). However, any such management options will inevitably be costly and thus even where practical can only be implemented in high-priority stands or locations that should be adequately evaluated at regional and landscape levels (Jump *et al.*, 2010).

Conclusions

While we have made substantial progress in understanding the proximate causes of tree mortality in recent decades, our ability to predict drought-induced mortality in space and time remains restricted. The present-day water resource requirements of woody species in any given area are strongly determined by historical factors including past climatic, disturbance and management legacies acting over decades to centuries. Current rapid environmental changes can, therefore, result in structural overshoot through the temporal mismatch of resource requirements from resource availability at local to regional scales. Improved understanding of structural overshoot drivers and processes ultimately will allow more refined model projections of potential dieback responses of Earth's forest ecosystems when combined with climate change and land use projections. Current climate projections of substantially warming temperatures and increased occurrence of extreme drought events and heatwaves (Cai *et al.*, 2015; Duffy *et al.*, 2015; Tebaldi & Wehner, 2016) suggest strong possibilities that current forests, adapted to historic climate regimes, could soon become structurally "overbuilt" for more stressful future climate episodes (Allen *et al.*, 2015; McDowell & Allen, 2015). Given the resulting potential occurrence of substantial overshoot-induced structural dieback responses, ranging from reductions in canopy leaf area and reduced tree heights to turnover of large trees (and even tree species) through mortality of dominant species, better projections of forest structural overshoot responses are essential for predicting changes to ecosystem functions from regional to global scales (Wei *et al.*, 2014; Frank *et al.*, 2015; Anderegg *et al.*, 2016b; Brouwers & Coops, 2016; Mascorro *et al.*, 2016).

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SUPPORTING INFORMATION

Appendix S1. Methods used for the literature review of co-drivers of drought-induced tree mortality.

Appendix S2. Studies reporting a temporal or spatial modification in the intercept and/or slope of self-thinning lines.

Appendix S3. Detailed description of case studies documenting drought-induced tree dieback responses relevant to the structural overshoot framework.

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