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Abstract

The surge in global efforts to understand the causes and consequences of drought on forest ecosystems has tended to focus on specific impacts such as mortality. We propose an eco-climatic framework that takes a broader view of the ecological relevance of water deficits, linking elements of exposure and resilience to cumulative impacts on a range of ecosystem processes. This eco-climatic framework is underpinned by two hypotheses: 1) exposure to water deficit can be represented probabilistically and used to estimate exposure thresholds across different vegetation types or ecosystems; and 2) the cumulative impact of a series of water deficit events is defined by attributes governing the resistance and recovery of the affected processes. We present case studies comprising *Pinus edulis* and *Eucalyptus globulus*, tree species with contrasting ecological strategies, which demonstrate how links between exposure and resilience can be examined within our proposed framework. These examples reveal how climatic thresholds can be defined along a continuum of vegetation functional responses to water deficit regimes. The strength of this framework lies in identifying climatic thresholds on vegetation function in the absence of more complete mechanistic understanding, thereby guiding the formulation, application and benchmarking of more detailed modelling.

Introduction

Increasing duration and intensity of soil water deficit and associated elevated temperature stress will elicit a range of vegetation responses across the spectrum of ecosystems (Breda *et al.*, 2006). These responses range in severity from reduced fecundity and seedling recruitment loss, reduced productivity, episodic mortality and ultimately to the potential for long-term change in species composition. Separately or as a whole, these effects will have consequences for carbon sequestration, water provision and maintenance of biodiversity (Adams *et al.*, 2012, Breda *et al.*, 2006, Redmond & Barger, 2013b). A recent meta-analysis of drought resistance among a diverse collection of woody plant species (based on measurements of their water transport system) concluded that all forest ecosystems may be similarly vulnerable to drought damage, regardless of their site conditions and climate (Choat *et al.*, 2012). While the study by Choat *et al.* (2012) considered only a narrow selection of traits that confer resistance to water deficit, it, and other global comparisons raise important issues regarding how we might evaluate both the physical dimensions of water deficit and the associated vegetation responses, in a consistent and holistic manner.

While interest in drought-induced tree mortality has highlighted the potential for severe impacts among a broad range of forest types, it is important to recognise that in most cases a single episode of water deficit does not induce catastrophic mortality. However, the cumulative impacts of either low frequency, high intensity and high frequency, low intensity water deficit may generate changes in ecosystem structure, composition and function over long-term time scales (van Mantgem *et al.*, 2009). For example, a reduction or cessation in seedling recruitment during a period of reduced rainfall may lead to subtle shifts in the population structure, and potentially restrict future recovery from more catastrophic events (Fensham *et al.*, 2015, Suarez & Kitzberger, 2008). Thus, evaluation of the degree to which the system is susceptible to adverse impacts of drought, requires consideration of the cascade of events that perturb the ecosystem, across a range of scales, drought intensities and durations.

Given the breadth of inputs potentially determining drought impact on ecosystems, attempts to determine relevant thresholds and feedbacks demand an approach that integrates elements of climatology and ecology (Anderegg *et al.*, 2013). Climatological studies predominately focus on climatic exposure (e.g. magnitude and duration of drought) and comparing trends in precipitation and temperature with relevant climate change projections (Burke *et al.*, 2006, Dai, 2013, Knapp *et al.*, 2015, Meehl & Tebaldi, 2004). However, interpreting how these climatic drivers, considered at typically continental or regional scales might impact plant functioning at finer scales, is a critical challenge in ecosystem science. Assessments of drought impacts often come from opportunistic observational studies (Ganey & Vojta, 2011, Matusick *et al.*, 2013) yield system-specific insights into changes in vegetation structure and composition after drought, but provide a limited perspective on the mechanistic basis for such impacts. Thus, it is difficult to use these studies to generalise across larger temporal and spatial scales. Experimental studies can help to define those mechanisms associated with water and carbon dynamics that limit plant function and survival (Mitchell *et al.*, 2013b, Sevanto *et al.*, 2013), but often do not reflect those elements of exposure that might be critical in provoking observed impacts (e.g. associated change in vapour pressure deficit) (Beier *et al.*, 2012). The lack of an integrative framework among these disparate approaches limits our capacity to model the outcomes of drought events in ecosystems. For example, processes such as recruitment, mortality and system recovery in response to water deficit are not particularly well represented by dynamic vegetation models (Gustafson *et al.*, 2015, McDowell *et al.*, 2013). These issues are emerging as critical knowledge gaps in the evaluation of cumulative impacts of water deficit, requiring the consideration of multiple processes across time scales that capture the full stress-induced decline and recovery dynamics of the system (Anderegg *et al.*, 2015).

Evaluating cumulative impacts of water deficit at higher levels of organisation, (e.g. impacts on stand productivity) requires a broader consideration of the inherent complexity of forest systems and their multifaceted responses. The vulnerability assessment framework adopted by the Intergovernmental Panel on Climate Change characterises the degree to which a system is susceptible to adverse effects and provides a useful starting point for integrating the relevant biophysical components (Schneider *et al.*, 2007). Under a vulnerability framework, impacts on forest systems from water deficit are a function of: 'sensitivity'; the degree to which the system will respond, 'exposure'; characteristics of the climate that deliver water stress and, 'adaptive capacity'; the degree to which a forest system can change to reduce the overall impact (Turner *et al.*, 2003). This framework would suggest predicting impact in a forest system using say a single dose-response type function may only partially capture the multi-dimensional response of ecosystem processes. This is because the impacts of water deficit on vegetation at any one time is dependent on the attributes of the current event (duration and intensity) as well as preceding events that can cause 'legacy' effects on the system while recovery to some pre-stress level of functioning occurs (Anderegg *et al.*, 2015). Thus, exposure to water deficit over multi-decadal time scales comprises a disturbance regime that includes the attributes of intensity, duration, timing and frequency (Fig. 1a). Likewise, the sensitivity and inherent adaptive capacity of vegetation to this disturbance regime is multi-dimensional and is more adequately described by concepts of 'resilience'.

Resilience is defined here as a function of both ‘resistance’; the capacity to maintain function during a period of water stress and ‘recovery’; the time required for the system to return to its pre-stress condition (Fig. 1b) (Hodgson *et al.*, 2015). Properties of resistance can be described by quantifiable parameters that represent thresholds of diminished productivity or damage to tissues or organs. Similarly, recovery involves the resumption of pre-stress function for a suite of processes that can be quantified with respect to duration of the recovery period.

An illustration of how these properties shape vegetation responses to water deficit in a north-eastern Australia savanna is presented in Figure 1. This example is based on an observed series of climatic water deficit events (exposure) and patterns in the fraction of absorbed photosynthetically active radiation (fPAR; vegetation function), an index that scales closely with gross primary productivity (Running *et al.*, 2004). The occurrence of two water deficit events with similar intensity (labelled as i and ii in Fig. 1) produces divergent responses because the occurrence of a less intense event (labelled as iii) within close succession to event (ii) i.e. inter-arrival period < recovery period, results in a larger reduction and recovery time of fPAR than the observed impact of a singular water deficit event (Fig. 1b). The key dimensions to these response dynamics can be formulated as a single function that integrates climate and ecosystem function. We define this as the “eco-climatic framework” that provides a generalised relationship between exposure and resilience according to the magnitude of loss of vegetation function (determined by a resistance function), the corresponding recovery time for a given loss of function and the influence of event timing (Fig. 2).

In this paper, we describe the key elements of this eco-climatic framework and demonstrate its application in assessing the vulnerability of different vegetation types to changes in climatic regime. This framework is discussed in the context of two hypotheses. 1) Exposure to water deficit can be represented probabilistically to estimate thresholds of key vegetation processes, and hence compare vulnerability of different vegetation types or ecosystems. 2) The cumulative impact of a series of water deficit events is defined by quantifiable attributes governing the resistance and recovery of the affected processes. We focus on four critical ecological processes; recruitment, plant productivity, canopy collapse and mortality and discuss quantifiable metrics that might be used to evaluate thresholds in their response to water deficit. The discussion is predominately focussed at the stand scale (areas of 100 – 1000 m^2), while recognising the contribution of drivers at much larger (e.g. regional climate,) or smaller (e.g. leaf-level physiology) scales. Two case studies are presented to demonstrate the utility of this framework, and to provide a biologically scaled representation of water deficit that can be used to assess ecosystem vulnerability by linking components of ecosystem exposure and resilience.

Exposure to water deficit

The term “drought” specifically refers to a set of exceptional conditions of water shortage, and conventional definitions of drought focus on societal impacts within a specific context such as water resource management or agricultural production (Mishra & Singh, 2010). Drought impacts on ecosystems tend to be more complex and difficult to define. For example, the term “drought” is often used to describe changes in water availability that are within the normal or mean local climate (e.g. seasonal drought in Mediterranean-type ecosystems), rather than as a period of climatic water deficit that is statistically exceptional and has the potential to push ecosystems beyond established tolerances to water stress. The distinction between drought and aridity, as either a condition capable of inducing stress responses beyond specific thresholds or a normal expression of a community’s water regime, is crucial in understanding plant adaptation and the likelihood of species shifts under future changes in water availability. In outlining a broader formulation of forest responses to water availability, we use the term “water deficit” (as opposed to drought) because it refers to any change in water availability that is capable of causing stress over a range of severities.

Climate-based measures of water deficit quantify the difference between precipitation and evaporation/evapotranspiration in absolute terms, or through standardisation routines using differing levels of complexity enabling comparisons among sites (Mishra & Singh, 2010). However, to be broadly applicable, stressful events at a given site need to be characterised using probabilistic approaches that can determine the significance of particular periods of water deficit, relative to the observed climatic distribution. In other words, a probabilistic approach can quantify how exceptional a particular period of water deficit is with respect to some ”normal” set of conditions, to which a particular plant population is adapted, irrespective of whether the site’s climate is predominately wet or dry. The relative intensity of water deficits in contrasting ecosystems can be compared using indices such as the standardised precipitation evapotranspiration index (SPEI)(Vicente-Serrano *et al.*, 2010) , or

Palmer Drought Severity Index (Dai, 2013). The SPEI is computed using a time-series (> 50 y) of monthly values of the climatic water balance (precipitation minus potential evapotranspiration) fitted using a probability density function to provide estimates of water deficit intensity for any month within the historic time series (by definition, larger climatic water deficits are represented by highly negative values) (See supplementary material S1 for more details). Assessing patterns in SPEI associated with observed impacts of water stress (e.g. vegetation die-off) can provide a top-down approach for defining climatic thresholds across a broad range of systems (Mitchell *et al.*, 2014). Two published reports of drought mortality events: 1) a Mediterranean woodland in south-western Australia, 2010-11 (Matusick *et al.*, 2013) and, 2) a Savannah woodland system in north-eastern Australia, 2001-2005 (Fensham & Fairfax, 2007) provide examples of vegetation die-off associated with extreme water deficit. The most extreme meteorological conditions (derived from the minimum monthly SPEI value) experienced during the mortality events represented 0.1 and 0.7 % probability of occurrence across the 110 year time-series for the Mediterranean woodland and savannah ecosystems, respectively (see Mitchell *et al.* 2014).

Conditions of below average rainfall often coincide with periods of high temperature and heat waves, a pattern that is evident at continental (Dery & Wood, 2005), regional (Vautard *et al.*, 2007) and local scales (Matusick *et al.*, 2013). Long-term patterns in the relationship between the intensity of water deficit and maximum temperature for a particular site can provide an indication of the likelihood of experiencing both dry and hot conditions (Fig. 3a). The joint distribution of these two drivers of plant stress can be fitted using bivariate distributions that map the likelihood of water deficit and maximum temperatures for the climatic envelope for a particular site (Fig. 3b) (Mitchell *et al.*, 2014). This approach provides a means to capture the nature of the dependency between hot and dry conditions and evaluate the combined likelihood of an event exceeding relevant thresholds of both high water deficit and high temperature (Fig. 3b). From this analysis, inferences can be made around the extent to which vegetation is exposed, and therefore adapted, to the combined stressors of water deficit and high temperature. For example, vegetation exposed to climates with low dependence between water deficit and maximum temperature will tend to experience dry and hot conditions infrequently, and may be far less adapted to these combined stressors than vegetation that is exposed to these conditions more frequently.

The majority of episodic mortality events across a broad range of biomes appear to be triggered by the co-occurrence of drought and high temperatures and/or heat waves (Allen *et* *al.*, 2010, Mitchell *et al.*, 2014), yet the physiological basis of stress from this interaction are not well understood. High temperatures and heat waves increase evaporative demand and dehydration of plant tissues (Pfautsch & Adams, 2013). Additionally, plants experiencing water stress are likely to be more sensitive to periods of heat stress because reduced transpiration-mediated cooling of the foliage results in increased heat loads on tissues and additional light stress (Valladares & Pearcy, 1997).

Longer term patterns in exposure can be characterised according to the frequency of events across a range of durations and intensities. One approach is to disaggregate the time-series of climatic water deficit across different averaging periods (Vicente-Serrano *et al.*, 2013) and identify discrete events based on a specific threshold probability (see McKee et al., 1993 for an example). Figure 4 presents time series of SPEI derived at three time scales (akin to averaging periods) to illustrate how different dynamics in water deficit might impede different processes according to their duration and frequency. Short duration (mean duration < 12 months) and highly frequent (every 1 – 2 years) water deficit events develop at shorter time-scales (< 6 months) and tend to affect those processes that are sensitive to small changes in soil water availability, such as recruitment. In contrast, intense water deficits (e.g. developing over 24 month time-scales), are more capable of inducing crown damage or forest mortality and are more rare (every seven years) and prolonged (mean duration of 33 months) (Fig. 4). Partitioning the scale of observation provides information on frequency, or return interval, for water deficit events of different duration and intensity and helps to establish how regularly a specific set of drought conditions must be tolerated, and the potential window of recovery. In many cases, the extant climatic record may be short relative to the lifespan of forests and the periodicity of extreme droughts associated with broad-scale mortality. Climatic reconstructions using proxy evidence (such as tree ring widths) may help to identify extreme drought events over a longer analysis period than the meteorological record (Anderegg *et al.*, 2015, Williams *et al.*, 2010).

Resilience

The capacity of a forest or vegetation community to tolerate, avoid and/or recover from potential stressful events is governed by its resilience (Hodgson *et al.*, 2015). Stress in this context is defined by any constraint associated with water deficits that limit plant function or resource acquisition (i.e. survival, carbon uptake or growth) (Grime, 1977). The broader scale climatic drivers of water deficit translate into stress or physiological water deficit via spatial and temporal variation in soil conditions, the presence of secondary stressors such as biotic agents and genetic/phenotypic variation among individuals (Fensham *et al.*, 2015, Jactel *et al.*, 2012, Sperry & Hacke, 2002). The contribution from one or more of these factors is critical in modulating the relative exposure threshold associated with a particular response, such as episodic mortality, meaning that individuals within a stand can potentially succumb across a range of water deficits and/or high temperatures (Fig. 2b). Thus, resilience to water deficit encompasses 'conditioning factors' that modulate the physiological water deficit as well as the biological dimensions of plant responses to water stress. To focus the discussion of plant responses to water deficit, we consider a set of quantifiable thresholds that have been shown to exert strong controls on vegetation function via changes in plant water and carbon balance. They include; recruitment failure involving both germination and seedling survival, cessation of primary productivity and its control via stomatal regulation and xylem cavitation and its influence on severe losses of biomass and mortality.

The spectrum of attributes controlling resistance and recovery

The resilience of forest stands to water deficit is dependent on traits and stand attributes that may slow and/or avoid reductions in water status, sustain physiological functioning at low water status and determine the rate of recovery when water deficits are relieved (Chaves *et al.*, 2002) (Fig. 5). The inherent resistance of plants to water deficit produces a 'physiological sequence' of responses controlled by a set of regulatory mechanisms that help to maintain a positive water and carbon balance (Fig. 5). The initial responses to water deficit (minutes to weeks) include stomatal closure, osmotic adjustment, cessation of growth and changes in carbon allocation and leaf biochemistry (Fig. 5). For the most part, these processes are highly dynamic and rapidly reversible (Fig. 5) and are associated with alterations in gene expression and metabolism (Peñuelas *et al.*, 2013). During protracted periods of drought stress (days to years), resistance is also defined by plastic responses that range from adjustments in hydraulic architecture, biomass allocation, and phenology (Fig. 5). For example, intraspecific plasticity in leaf area and sapwood area to leaf area ratios appear to be a major determinant of how populations respond to climate (Martin-StPaul *et al.*, 2013, Mencuccini & Grace, 1994) and single drought events (Pook, 1986). Furthermore, structural changes that promote homeostasis of water status may be particularly important, where there is limited plasticity in leaf physiological responses and parameters associated with cavitation resistance (Martínez-Vilalta *et al.*, 2009). These responses can promote acclimation by enhancing resistance to subsequent stress at both the individual- or stand-level.

Mortality of seedlings (recruitment failure) and mortality of adults may occur under different levels of water deficit yet the process may be similar (Fig. 5). The specific pathway leading to death is thought to involve a breakdown in water transport; entry of air into the xylem tissues (cavitation) preventing water movement across the plant, and/or carbon metabolism; assimilation of carbon and transport and use of carbohydrates for physiological functioning (McDowell *et al.*, 2011, Mencuccini *et al.*, 2015) . Widespread mortality responses can lead to lasting impacts on stand dynamics and may cause shifts in community composition and the contraction of species ranges over longer time frames (decades to centuries)(Fensham *et al.*, 2015) (Fig. 5).

Short-term recovery from water deficit and associated stressors involves the resumption of gas exchange through stomatal opening and repair of biochemical processes (e.g. membrane transport, carbon and nitrogen metabolism). At longer time scales, remobilisation of stored carbohydrates is critical for regrowth of tissues either shed during drought (Palacio *et al.*, 2012) or damaged by embolism (Brodribb *et al.* 2011) or by biotic attack provoked by water stress (Fig. 5). After significant loss of above and below ground biomass, complete recovery may require significant storage pools of carbohydrates over months to years (Radosevich & Conard, 1980). Germination and recruitment strategies are important for resilience and may occur in concert or as an alternative to resprouting strategies. In some cases, sustained water deficits can stimulate flowering and seed production (Breda *et al.*, 2006) that may act to accelerate recovery, if post-drought conditions are suitable. Those functional traits that enable recovery from a single event may be heavily dependent on plant condition and vigour that reflect the stress legacy and acclimation to the prevailing water deficit regime (Niinemets, 2010).

Conditioning factors and secondary stressors

Conditioning factors such as soil characteristics and species interactions, size/age effects, acclimation potential and characteristics of host and habitat suitability (Raffa *et al.*, 2008), and time since the previous disturbance, all influence the development and onset of the water deficits, thereby determining the resilience of the system (Lloret *et al.*, 2012). These conditioning factors can be critical. For example, soil water deficits within the root zone of smaller plants may escalate rapidly given their reduced rooting volume relative to total leaf area, whereas larger trees remain relatively buffered by a larger rooting volume (Duursma *et al.*, 2011). Hence, plant size and age can be important determinants of the rate at which water deficit limits survival within stands (Lloret *et al.*, 2004); e.g. seedlings may be more (or less) sensitive to regimes (at a given frequency, intensity or duration) than older/larger cohorts.

Changes in exposure can also promote interactions with secondary stressors such as biotic agents that can yield antagonistic, additive or synergistic outcomes for plant health and vigour (McDowell *et al.*, 2008, Mitchell *et al.*, 2013a). Multiple stress interactions arising during water deficit are common across many vegetation types (Niinemets, 2010) and their impact may be strongly dependent on the intensity and duration of water deficits (Bansal *et al.*, 2013, Raffa *et al.*, 2008).

Defining impact: interactions between exposure and resilience

The cumulative impacts of water deficits on forest stands are presented within the eco-climatic framework in terms of the four quantifiable key thresholds discussed above (Fig. 6). To provide a simplified representation of this exposure-resilience type function, exposure is considered in terms of the intensity of water deficit events using a probabilistic distribution (based on SPEI, as discussed above) (Fig. 6). Monthly water deficit intensity or SPEI values occurring less frequently (towards the tails of the distribution) represent either exceedingly wet or dry conditions; here, we focus on the dry end of this distribution (Fig. 6). A guiding principle of the eco-climatic framework maintains that the impact of a single water deficit event can be viewed as part of a broader rainfall/water deficit regime resulting in a continuum of potential impacts, ranging from common, mild water deficits with impacts on recruitment to infrequent and severe events generating large-scale tree mortality (Breshears *et al.*, 2009). Based on previous studies, we estimate that a water deficit intensity equivalent to a monthly climate water balance value <2% probability of occurrence relative to the observed distribution, represents an exposure sufficient to induce canopy collapse within the mature members of the population (Mitchell *et al.*, 2014). While these hypothesised estimates of exposure thresholds (expressed as percentiles) are available for some processes, our case studies (provided below in this paper) elucidate how we might integrate observation and modelling to populate these functions further.

The magnitude of ecosystem response to drought is represented here by the half-time of recovery. When this half-time approaches infinity, it is assumed that a permanent change in either the species composition or structure has occurred (Fig. 6c). Brodribb and Cochard (2009) showed that the rate of recovery of plant functioning to pre-drought levels (expressed as $t^{-1/2}$), in their case plant water transport system, followed a close relationship with the intensity of plant water stress. This type of formulation can also be applied at the stand scale. An example of slow recovery is seen in *Eucalyptus* woodlands in semi-arid environments in Australia where severe droughts have resulted in 90% tree death over limited areas and more than 25% of trees killed at regional scales (Fensham & Holman, 1999). *Eucalyptus* species in these communities are long-lived and have very limited seed dispersal (Fensham *et al.*, 2005). Thus, recovery is a protracted process with a half-time of many centuries as surviving trees regenerate and produce young trees that need to mature, before gradually dispersing from the local surviving trees.

The aggregate impact on ecosystem processes is also affected by multiple feedbacks that act to reinforce changes in structure and function. For example, the shedding of foliage and branches may increase fuel load and fire severities in stands where tree density and cover is already diminished. Changes in microclimate can also be dramatic after tree mortality events and increase energy and light penetration into the understorey (Royer *et al.*, 2010). The altered microclimate associated with drought events may alter recruitment patterns, particularly for those species that require shading for establishment (Redmond & Barger, 2013a).

Case studies: linking exposure and resilience

The eco-climatic framework proposed here considers that the resilience of key processes for a forest stand can be described using a probabilistic representation of exposure and corresponding thresholds on vegetation function (Fig. 6). The following case studies provide an application of this framework using two species (*Eucalyptus globulus* and *Pinus edulis*) from contrasting environments and with contrasting ecological strategies. *Eucalyptus globulus* is a temperate species common to Tasmanian forests, capable of resprouting after drought and fire; this case study uses stands near Hobart, Tasmania that experienced sustained canopy damage and mortality during the summer of 2012-13 (Mitchell *et al.*, 2014). The second case study uses *Pinus edulis*, a species that occurs in semi-arid environments in the south-western United States, regenerates from seed and has limited capacity to recover from hydraulic failure (Breshears *et al.*, 2009, Royer *et al.*, 2011). Episodic mortality has been observed in *P. edulis* populations across south-western United States and this study uses stands near Los Alamos, New Mexico, which were monitored in Breshears *et al.* (2009). We integrate existing ecophysiological knowledge with the probabilistic descriptions of water deficit outlined above, to evaluate the likelihood of biotic thresholds under observed and future climate regimes. The analysis and discussion addresses key components of the eco-climatic framework (Fig. 7):

1. Exposure was characterised in terms of the water deficit intensity represented in terms of monthly probabilities, using a climatic water balance; SPEI, computed for observed (1961 - 2013) and future climate projection (2010 – 2050; CSIRO Mk 3.5).
2. Resistance thresholds of three processes (recruitment, productivity and canopy collapse) were derived from empirical and mechanistic models and used to biologically-scale water deficit intensity to different climate regimes (see S2, S3 and S4 for detailed method description).

By combining species resistance thresholds based on stomatal and hydraulic controls with field data that captures the ‘plants eye’ view in response to water deficit, we were able to define relevant response functions that linked exposure (water deficit intensity) and levels of resistance of various processes (Fig. 7). The thresholds for climatic exposure derived from this approach represent likelihoods of occurrence (over a 113 yr period) of SPEI at 18 % for recruitment failure (although recruitment was also limited by other factors during periods of higher water availability); SPEI 8 % for cessation of productivity and SPEI 2% for canopy collapse (Fig. 7 and Fig S3). The probability estimate of 2% for canopy collapse (based on P50) is consistent with previous analyses of other Australian ecosystems, where canopy collapse or mortality occurred when drought intensity was less than 2% probability (Mitchell *et al.*, 2014). Based on similar response functions, *P. edulis* had thresholds corresponding to 33%, 9% and 1% probability of occurrence for recruitment, zero carbon assimilation and P50, respectively (Fig. S4).

This approach provides a basis to assess future impacts of water deficit regimes and their likelihood of exceeding key thresholds for vegetation function. For the *E. globulus* case study, changes in drought frequency and intensity from the observed 1974 – 2013 baseline to the projected 2011 – 2051 climate, resulted in an increase in the number of months for all three processes; 33%, 6% and 55% for recruitment failure, cessation of productivity and canopy collapse, respectively (Fig. 8).

While the impact of water deficit in these case studies was considered primarily in terms of resistance traits, mechanisms of recovery as outlined in Fig. 5 are critical for evaluating the dynamics of the response in its entirety. Given the contrasting ecological strategies of the two species presented in these case studies, the capacity for recovery of recruitment, productivity and canopy collapse may be considerably different. Although we observe slightly higher frequency of droughts capable of inducing canopy collapse in *E. globulus*, the loss of canopy functioning may be relatively short, if followed by relatively rapid recovery via resprouting (Zeppel *et al.*, 2015). Only during rarer, more intense events, may drought-induced mortality occur via systematic hydraulic failure. By contrast, the limited capacity of *P. edulis* for regrowth and a greater tendency for carbohydrate depletion during water deficit (Adams *et al.*, 2013), suggests that sustained loss of hydraulic function in the canopy is likely to represent a threshold capable of inducing whole-tree mortality (Brodribb & Cochard, 2009). These assertions emphasise the need for future studies to strengthen our understanding of the trade-offs between resistance and recovery mechanisms, and their contribution to ecosystem resilience more broadly.

Conclusion

An enduring challenge in the assessment of ecological disturbance is predicting the aggregate impact of an event or disturbance regime by scaling the relevant functional responses of individual organisms to the population and ecosystem level. Critical to understanding the adaptive capacity of species to water availability involves resolving misconceptions surrounding the significance of aridity (in terms of mean patterns of water availability) *versus* periods of water deficit occurring outside the normal set of conditions.   The first hypothesis addressed by this framework states that exposure to water deficit can be represented probabilistically and used to estimate exposure thresholds of key vegetation processes across different vegetation types or ecosystems. The case studies and other recent studies (Mitchell *et al.*, 2014) show that water deficits that are capable of severe impacts, such as canopy collapse and mortality, are associated with relatively similar extremes in exposure (e.g. SPEI < 2 % probability) suggesting a convergence in exposure thresholds for more extreme impacts among different vegetation types. A more comprehensive appraisal of the first hypothesis should consider a systematic approach to assessing spatial and temporal variation in thresholds such as embolism resistance (Anderegg, 2015). This may require new methods to rapidly evaluate and monitor plant conditions such as water status over multiple water deficit cycles of differing duration and intensity. Nevertheless, the strength of this framework lies in identifying climatic thresholds on vegetation function in the absence of more complete mechanistic understanding, thereby guiding the formulation, application and benchmarking of more detailed modelling (Meir *et al.*, 2015).

The second hypothesis underpinning the eco-climatic framework states that the impact of a water deficit event produces a change in vegetation function described by two key properties of resilience: the magnitude of the response of some process (resistance) and the time for recovery. While the two case studies in this paper evaluate the resilience of tree stands based on resistance traits, the extent to which recovery determines impact requires further investigation. This is a key knowledge gap that is hindered by the limited consideration of relevant species-specific traits that determine recovery within a broader definition of the impacts of water deficits (Fig. 6). Future research directed towards understanding the key dimensions of the trade-off between resistance and recovery will significantly improve our ability to assess vegetation responses over meaningful time frames.

We argue that resilience can be better understood by viewing changes in system function with respect to the water deficit regime and the impacts across multiple ecological processes, simultaneously. For example, an infrequent, intense drought event may kill only 10 % of the adult population, but if recruitment has been restricted or non-existent over the longer-term, the resilience of the population may be very low (Fig. 5). Thus, the cumulative impact of a water deficit regime can represent more severe consequences for ecosystem function (e.g. carbon and water budgets) than what might be predicted from a single extreme event. Modelling the long-term consequences of impacts from water deficit requires approaches that consider the system as a hierarchy of processes that react and recover to water deficits over differing temporal and spatial scales.

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Supporting Information Captions

S1: Methods for Fig. 1

S2: Methods for case studies

S3: Schematic of the biological scaling of climate data based on ecophysiological responses of *Eucalyptus globulus* to water deficit

S4: Schematic of the biological scaling transformation of climate data based on ecophysiological responses of *Pinus edulis* to water deficit

S5: Results from the biological scaling of water deficit intensity based on three ecophysiological thresholds

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Figure captions

Figure 1. Temporal patterns of water deficit define the exposure regime and associated impacts on plant function for a savanna woodland in north-eastern Australia. (a) Time series of climatic water deficit intensity (derived from the standardised precipitation evapotranspiration index; SPEI, 12 month time scale) for values < 33 % probability (red; (corresponding to SPEI < -1), and extreme values of < 2 % probability (dark red; corresponding to SPEI < -2). More negative values represent larger climatic water deficits and a lower likelihood of occurrence. The key aspects of exposure to water deficit include the intensity, duration, frequency and timing. (b) Time series of the fraction of photosynthetically active radiation (fPAR; 12 month moving average), used as a proxy for vegetation function (see fig. S1 for details). For a single event (labelled i), the shape of the response is defined by the properties of the vegetation's resilience (i.e. resistance to the stress and recovery time). The magnitude of the response (change or loss of vegetation function) is a property of vegetation resistance (red vertical arrow) and the time for vegetation function to return to some pre-stress level is a property of recovery (diagonal blue arrow). Impact is derived from the cumulative loss of vegetation function through time. The arrival of event (iii) in close succession to event (ii) demonstrates how the arrival of multiple water deficits can significantly increase the overall impact if recovery is incomplete.

Figure 2. The eco-climatic framework describes a generalised relationship between exposure to climatic water deficit and vegetation resilience. (a) The magnitude of change in function in response to a single event (i) is described by a dose-response type function, where water deficits of increasing intensity generate increasing change/loss of function according to the resistance of the forest stand. (b) The time to recovery to some pre-stress level of function

increases with the magnitude of the response. If the arrival of a second event (ii) occurs after the stand has recovered from event (i) then its magnitude and recovery can be estimated from the intensity of this event in isolation. Conversely, if event (ii) occurs in close succession to event (i) (i.e. inter-arrival time < recovery time), then the overall magnitude and corresponding recovery times is cumulative and results in larger impacts than the impact of the two events separately (i.e. the magnitude and recovery time is a function of event (i) and (ii) and their interaction).

Figure 3. Relationship between water deficit and high temperature are key dimensions for describing thresholds on vegetation function during stress. (a) Scatter plot of monthly climatic water deficit index *versus* maximum temperature index (1891 - 2013) from a tropical savanna site in north-eastern Australia. Data are fitted with a linear function (dashed line; r^2 = 0.20). (b) The fitted joint probability density of water deficit and maximum temperature indices shown by three contour lines denoting probability densities of 0.15, 0.05 and 0.02 percentiles (see text for details). The blue horizontal and vertical dashed lines are added to (b) to show the 0.02 and 0.98 percentiles for the singular distributions for water deficit and maximum temperature index. The double-headed arrow in panel (b) denotes a range in exposure thresholds for tree die-off across the bivariate distribution to illustrate how variation in resilience among individuals in a stand may shift through time and space.

Figure 4. Meteorological water deficit regimes can be characterised at multiple time-scales. (a) Filled contour plot of a climatic water deficit index; standardised precipitation evapotranspiration index (SPEI) computed for a range of time scales (1 – 48 months) plotted from 1964 – 2013 for Hobart, Tasmania. Highly negative SPEI values represent a large deficit between precipitation and potential evapotranspiration. Three dashed horizontal lines are drawn to represent examples of relevant time scales capable of affecting (i) 24 months - tree survival; (ii) 6 months - forest growth; and (iii) 3 months - recruitment. (b) Horizon plots of SPEI time series showing all values < 18% (red) and < 2% (dark red) probability of occurrence, corresponding to the three different time scales (i - iii) shown in (a). The frequency of events and mean duration are given for the analysis period (events are defined as any period reaching SPEI<18%, with its duration starting when SPEI <50% and ending when SPEI >50%).

Figure 5. An overview of some key components of the spectrum of resistance and recovery attributes that govern vegetation responses to water deficit. (a) Idealised probability distribution function of water deficit intensity (at the dry portion of the distribution) that reflects a range of events capable of inducing different impacts on ecosystem processes. The resistance and recovery of these processes is controlled by different attributes (b) that operate at a range of temporal scales (c) (represented by horizontal bars). Here, we assume that as water deficit intensifies the severity of the response increases. While recovery of the system to mild impacts such as a cessation in productivity may be dependent on short-term revival of gas exchange and assimilation, recovery from severe impacts such as canopy collapse or mortality will depend on mechanisms operating at longer time scales, such as resprouting and repair of the water transport system via new growth.

Figure 6. The impact of water deficit on four key ecosystem processes within the eco-climatic framework for a hypothetical forest stand. (a) Increases in water deficit intensity affect different processes according to their thresholds of resistance, resulting in larger declines in vegetation function. (b) Exposure is expressed as the likelihood for a particular intensity of climatic water deficit. (c) The recovery to the pre-stress condition can be defined by its half-time to recovery, whereby water deficit events with increasing impact have increasingly greater recovery half-times. Estimates of probabilities and corresponding return intervals of four water deficit events, represent the level of water deficit required to surpass the four thresholds associated with recruitment, primary productivity, canopy collapse (loss of above-ground tissues) and mass mortality are also shown. The dashed-dotted lines in (a), (b) and (c) represent a hypothetical shift in exposure scenario (i.e. a hotter, drier climate), potentially increasing the frequency and intensity of water deficit events and increasing the likelihood and magnitude of the loss of function and longer recovery times (denoted by arrows).

Figure 7. Overview of the approach used to link components of resilience of three processes; recruitment, productivity and canopy collapse, to exposure to water deficit. (a) Species resilience is defined by three thresholds from three different data sets, including a mechanistic model of recruitment and empirical relationships for productivity; leaf water potential *versus* stomatal conductance (*x*-intercept) and canopy collapse; leaf water potential *versus* percentage loss of leaf hydraulic conductance (50%). (b) Resilience and exposure are linked by biologically-scaling data to estimate the likelihood of reaching the three thresholds. The probability thresholds are labelled on the probability density functions of the monthly water deficit intensity and include (i) recruitment (18 %), (ii) productivity (8 %) and (iii)

canopy collapse (2 %). (c) Exposure is derived from a probabilistic representation of time series of water deficit intensity (SPEI values) for the observed record (1891 – 2012) (see text and supplementary information S2 and S3 for details).

Figure 8. Cumulative number of months, when three key thresholds are surpassed over an observed (1974 – 2013) and projected (2011 – 2050; CSIRO Mk 3.5) time series, at a site near Hobart, Tasmania. (a) Recruitment failure; (b) cessation of productivity and (c) canopy collapse.

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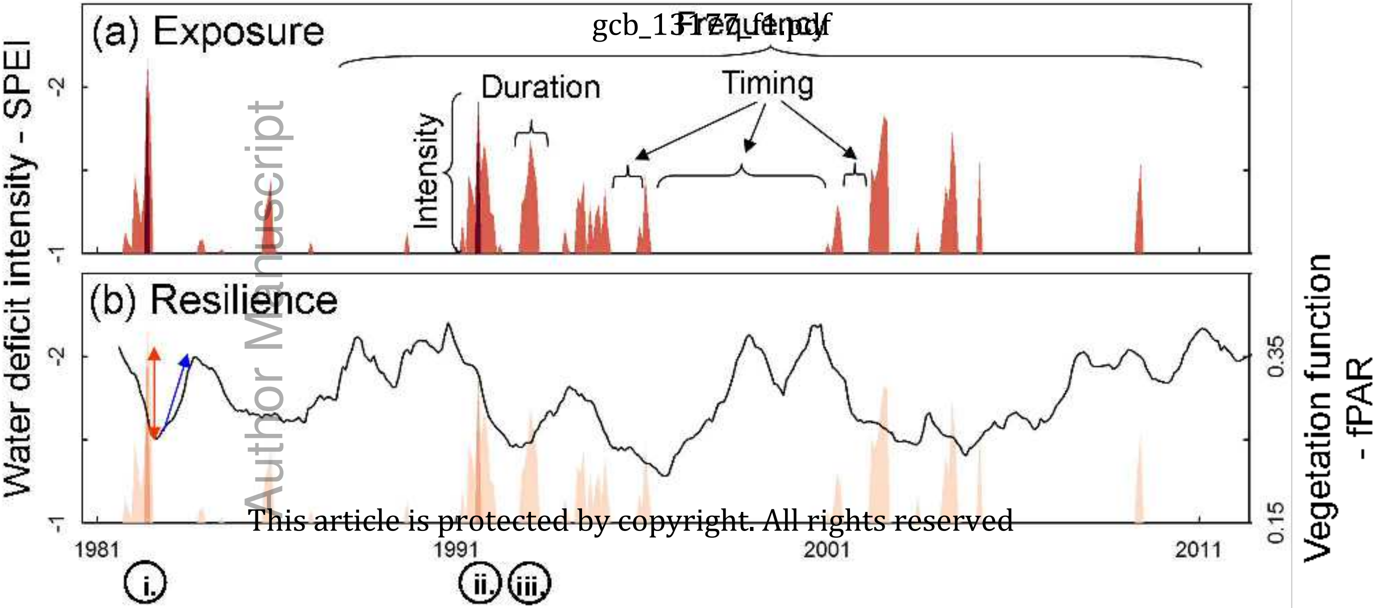

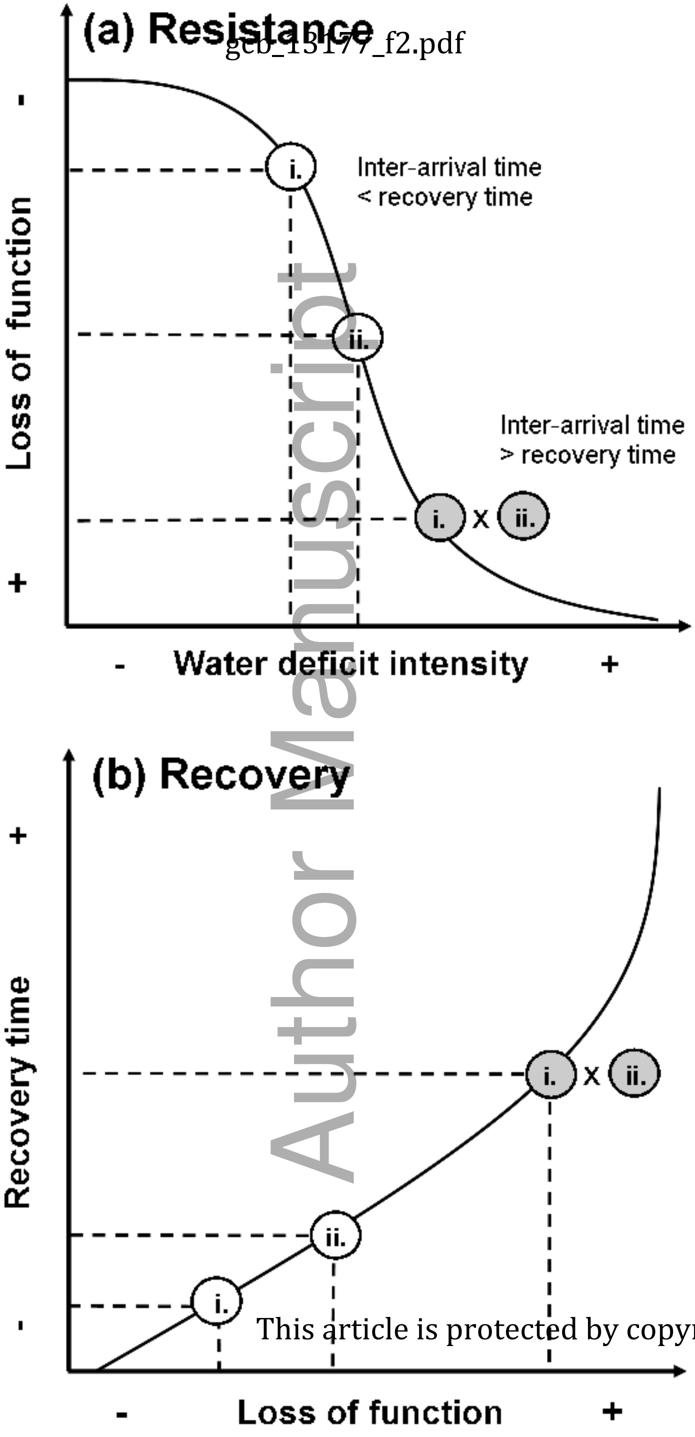
(a) Resistance
Loss of function
-
+
Water deficit intensity
-
+
i.
ii.
Inter-arrival time
< recovery time
Inter-arrival time
> recovery time
i.
x
ii.
(b) Recovery
Recovery time
+
-
Loss of function
-
+
i.
x
ii.
ii.
i.

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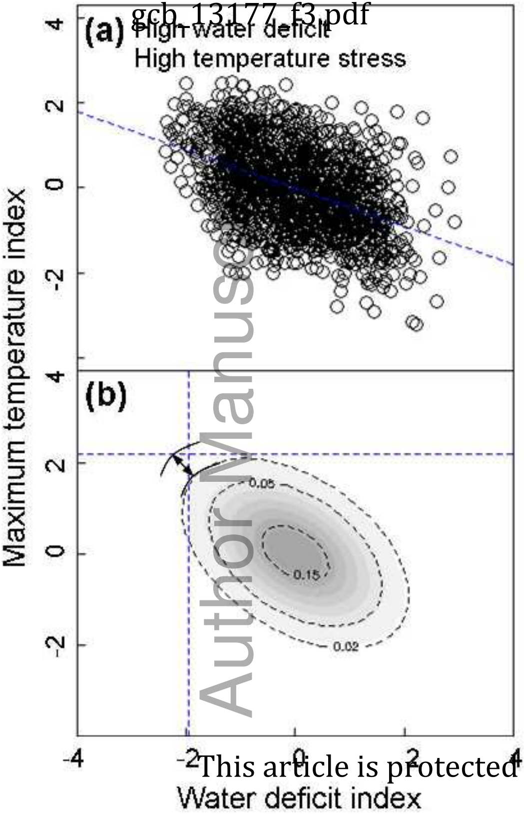
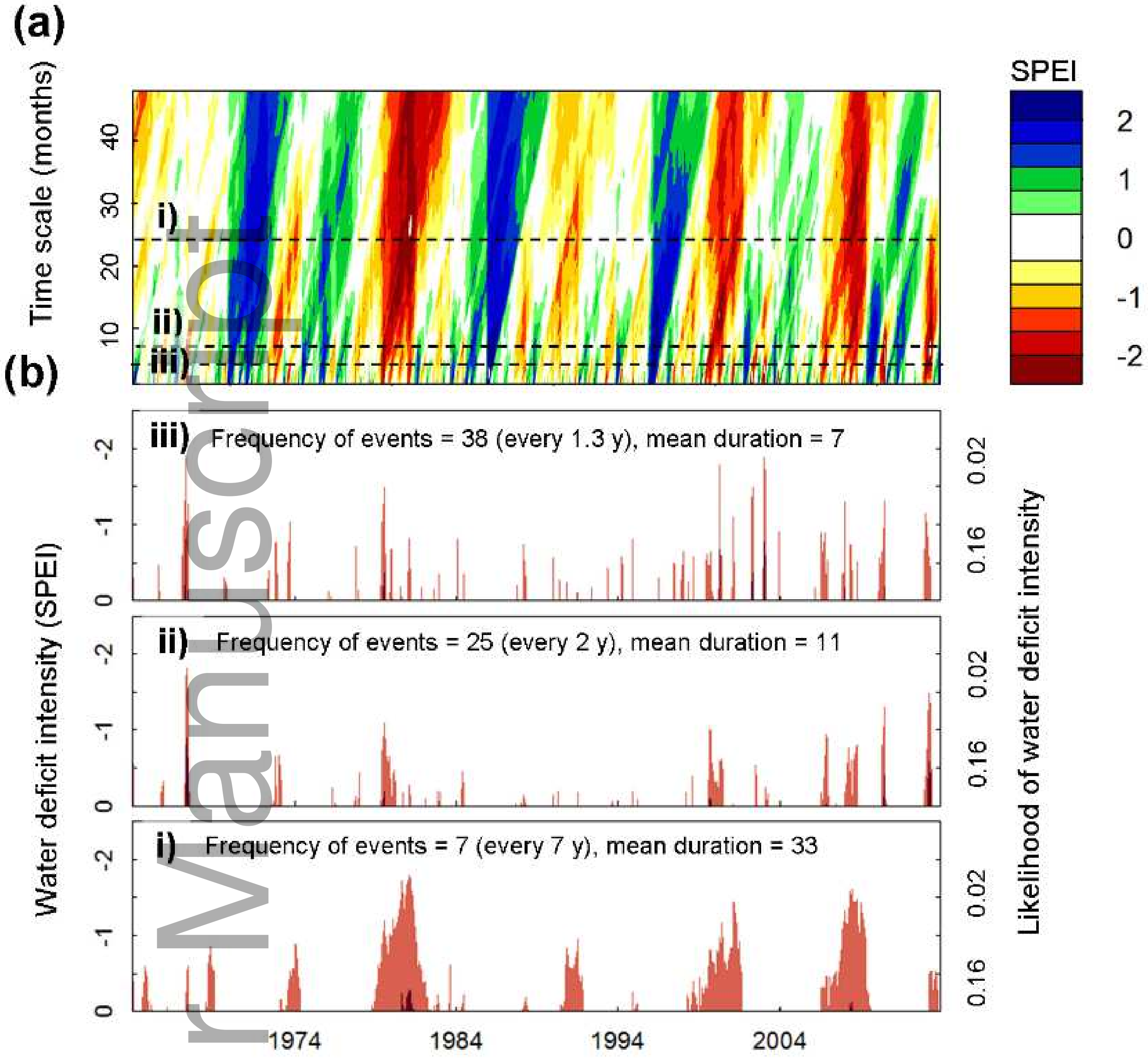
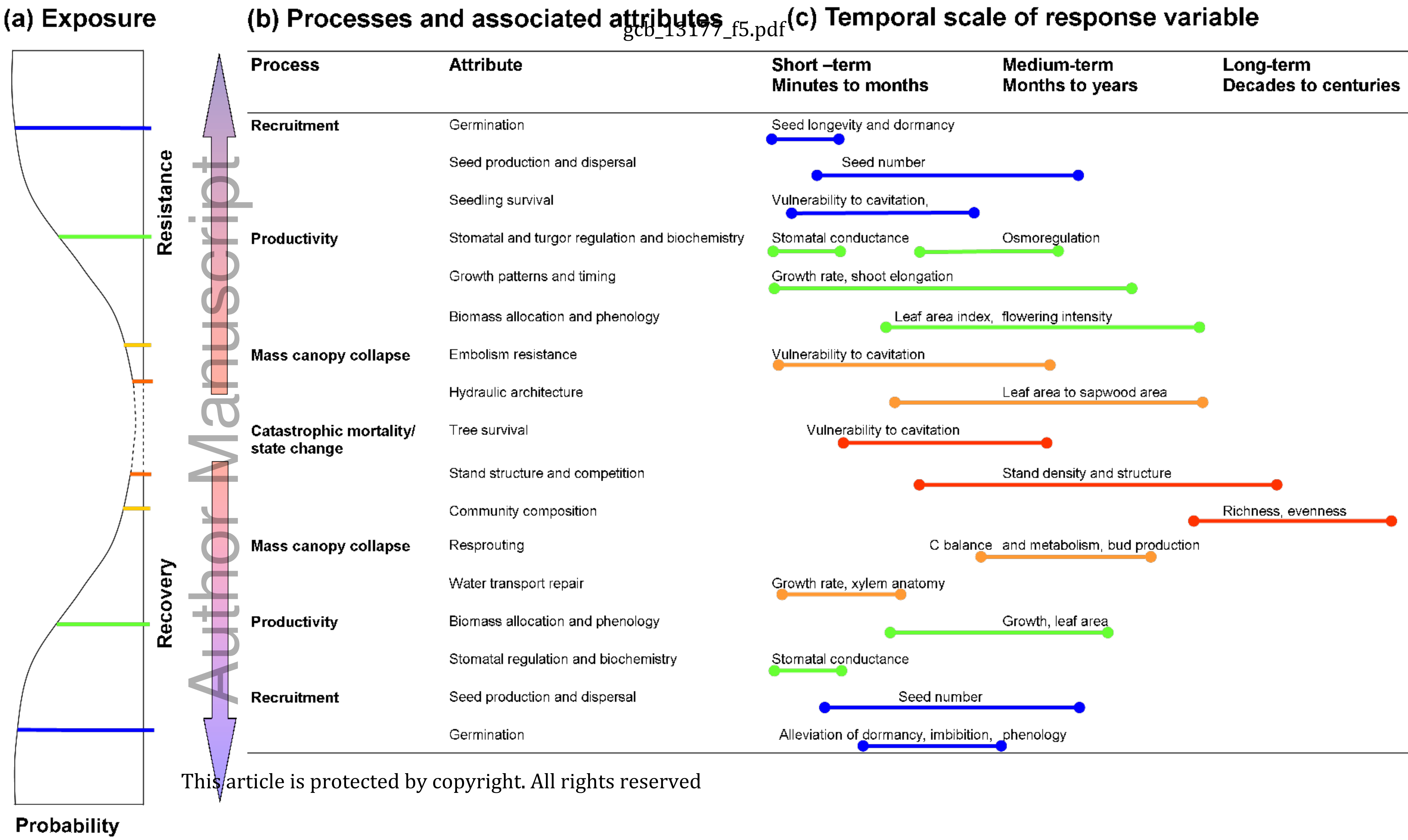



(a)
Time scale (months)
10
20
30
40
i)
ii)
iii)
SPEI
2
1
0
-1
-2
(b)
Water deficit intensity (SPEI)
Likelihood of water deficit intensity
iii) Frequency of events = 38 (every 1.3 y), mean duration = 7
ii) Frequency of events = 25 (every 2 y), mean duration = 11
i) Frequency of events = 7 (every 7 y), mean duration = 33
0
-1
-2
0.16
0.02
1974
1984
1994
2004


(a) Exposure
(b) Processes and associated attributes
(c) Temporal scale of response variable
Probability
Resistance
Recovery
Process
Attribute
Short –term
Minutes to months
Medium-term
Months to years
Long-term
Decades to centuries
Recruitment
Germination
Seed longevity and dormancy
Seed production and dispersal
Seed number
Seedling survival
Vulnerability to cavitation,
Productivity
Stomatal and turgor regulation and biochemistry
Stomatal conductance
Osmoregulation
Growth patterns and timing
Growth rate, shoot elongation
Biomass allocation and phenology
Leaf area index, flowering intensity
Mass canopy collapse
Embolism resistance
Vulnerability to cavitation
Hydraulic architecture
Leaf area to sapwood area
Catastrophic mortality/ state change
Tree survival
Vulnerability to cavitation
Stand structure and competition
Stand density and structure
Community composition
Richness, evenness
Mass canopy collapse
Resprouting
C balance and metabolism, bud production
Water transport repair
Growth rate, xylem anatomy
Productivity
Biomass allocation and phenology
Growth, leaf area
Stomatal regulation and biochemistry
Stomatal conductance
Recruitment
Seed production and dispersal
Seed number
Germination
Alleviation of dormancy, imbibition, phenology

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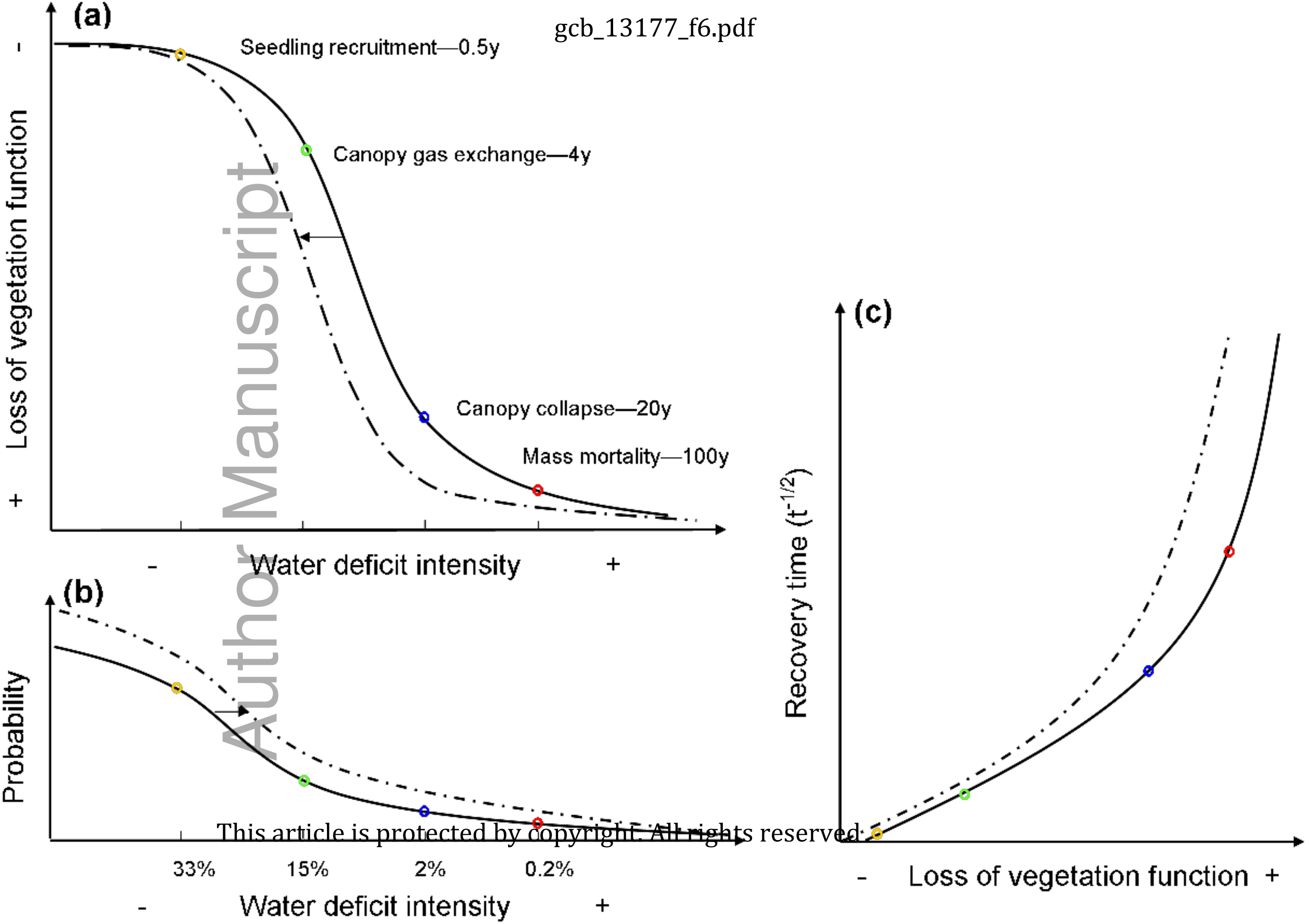
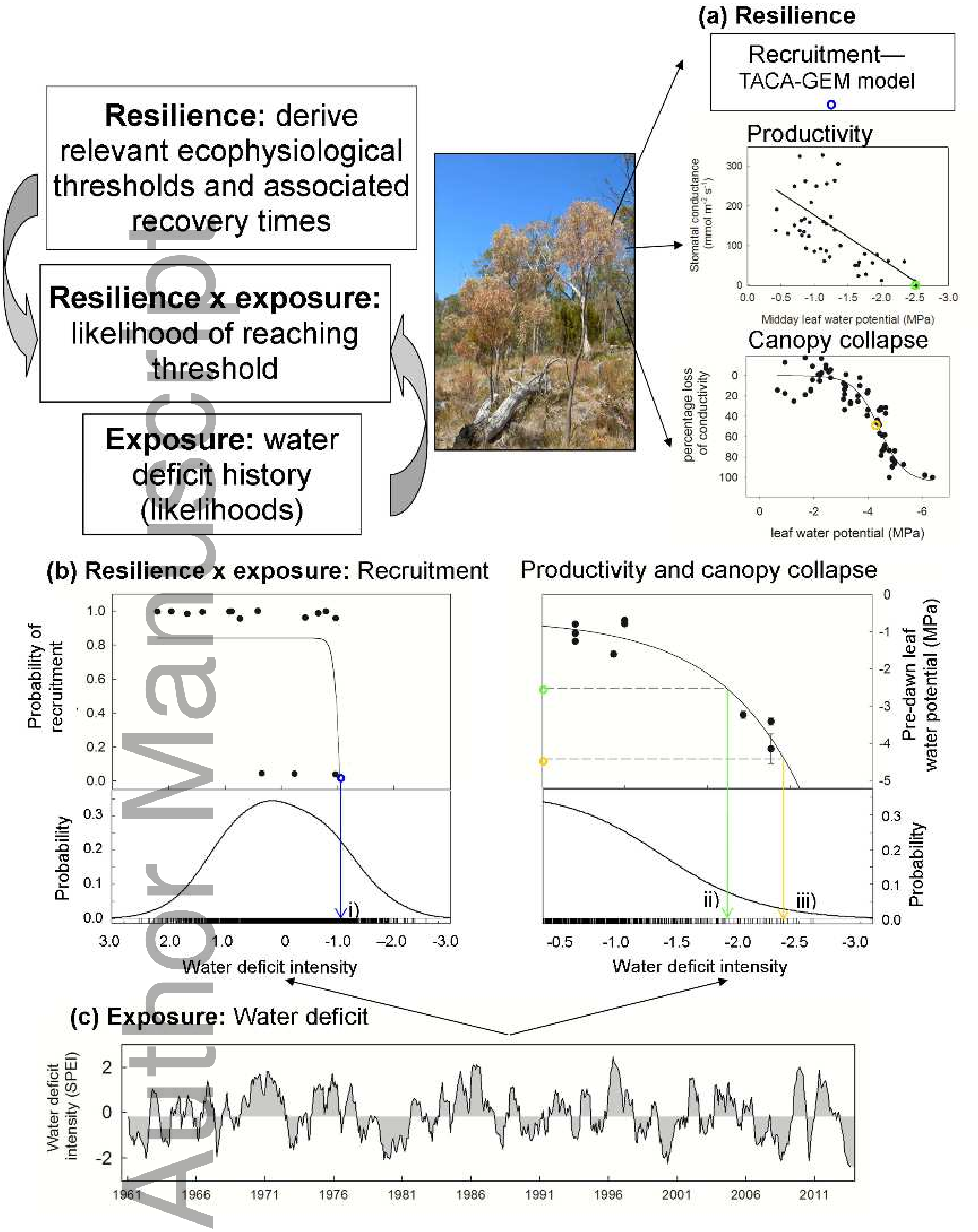
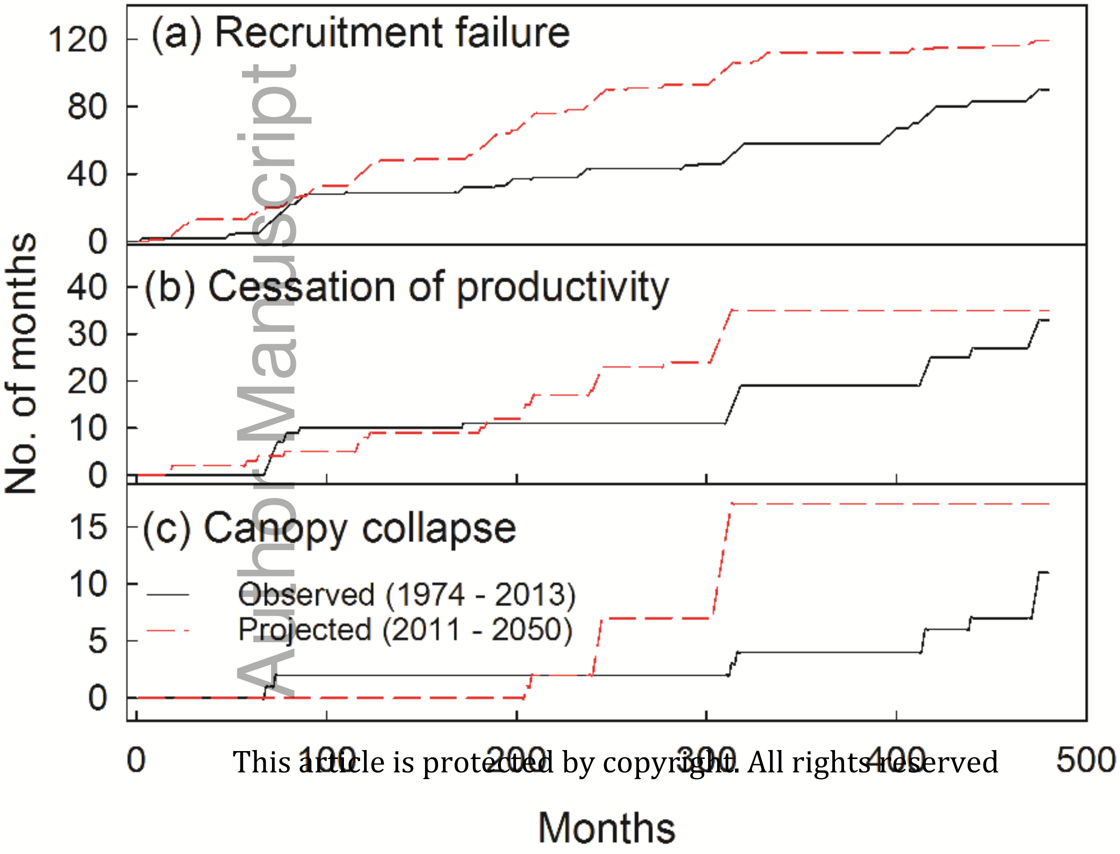



(a) Resilience
Recruitment—
TACA-GEM model
Productivity
Stomatal conductance (mmol m^{-2} s^{-1})
300
200
100
0
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
Midday leaf water potential (MPa)
Canopy collapse
percentage loss of conductivity
0
20
40
60
80
100
0
-2
-4
-6
leaf water potential (MPa)
Resilience: derive relevant ecophysiological thresholds and associated recovery times
Resilience x exposure: likelihood of reaching threshold
Exposure: water deficit history (likelihoods)
(b) Resilience x exposure: Recruitment
Probability of recruitment
1.0
0.8
0.6
0.4
0.2
0.0
Probability
0.3
0.2
0.1
0.0
i)
3.0
2.0
1.0
0
-1.0
-2.0
-3.0
Water deficit intensity
Productivity and canopy collapse
Pre-dawn leaf water potential (MPa)
0
-1
-2
-3
-4
-5
Probability
0.3
0.2
0.1
0.0
ii)
iii)
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
Water deficit intensity
(c) Exposure: Water deficit
Water deficit intensity (SPEI)
2
0
-2
1961
1966
1971
1976
1981
1986
1991
1996
2001
2006
2011


(a) Recruitment failure
120
80
40
0
(b) Cessation of productivity
40
30
20
10
0
(c) Canopy collapse
15
10
5
0
Observed (1974 - 2013)
Projected (2011 - 2050)
No. of months
0
100
200
300
400
500
Months