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## TERN, Australia's land observatory: addressing the global challenge of forecasting ecosystem responses to climate variability and change

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## Environmental Research Letters



## LETTER

## TERN, Australia's land observatory: addressing the global challenge of forecasting ecosystem responses to climate variability and change



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Supplementary material for this article is available [online](#)

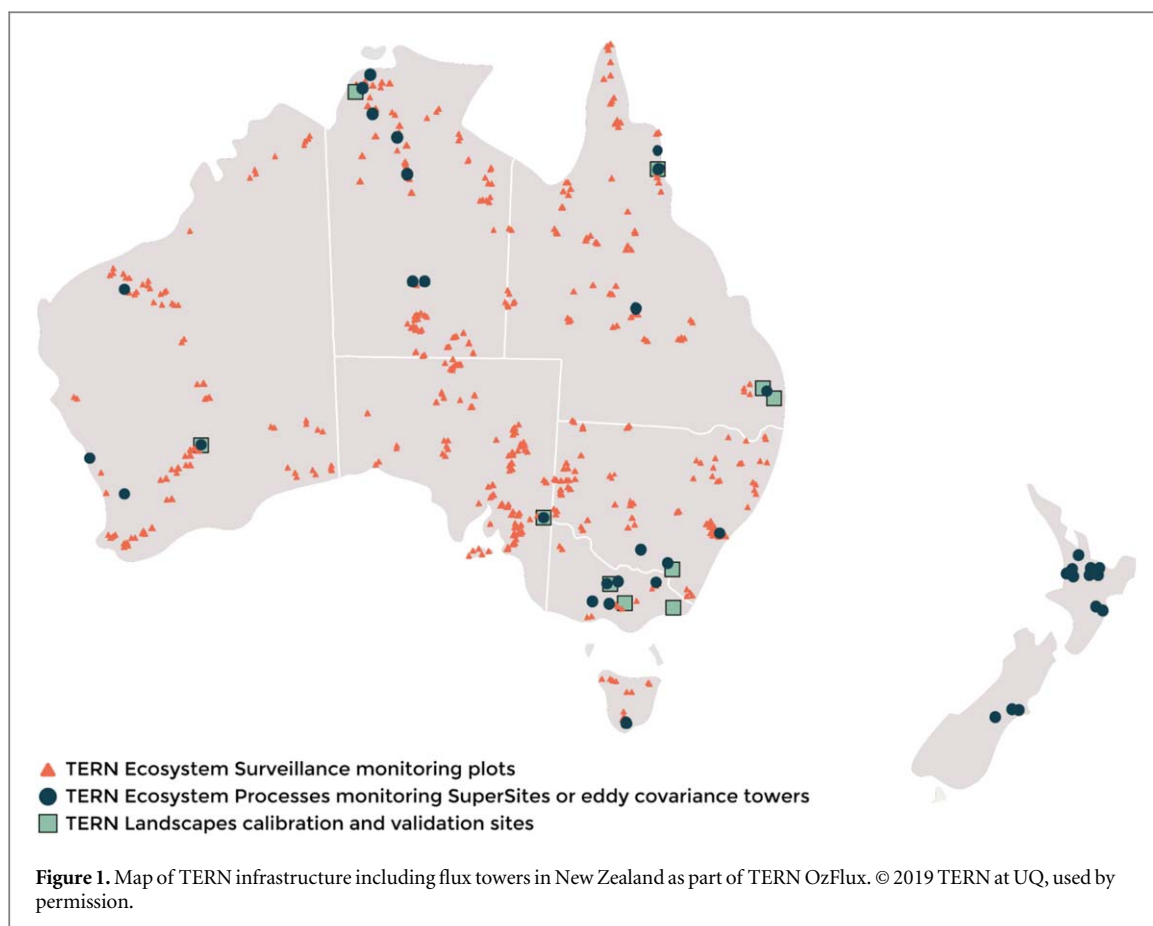
**Abstract**

The global challenge of understanding and forecasting ecosystem responses to climate extremes and climate change is addressed in this review of research enabled through environmental research infrastructure (RI) provided by Australia's Terrestrial Ecosystem Research Network (TERN). Two primary climatic drivers of ecosystem structure and function in Australia are fire and aridity, to which Australian flora and fauna have shown marked adaptability. Australian vegetation shows resilience to climate extremes of flooding rains, droughts and heatwaves such that variability in primary productivity of Australian vegetation has a tangible effect on the global carbon cycle. Nonetheless, Australian flora and ecosystems could be vulnerable to projected climate change (e.g. to increasing vapour pressure deficit). Refugia are also vulnerable to climate change, with conditions in these areas already near the tipping point for a change in community composition. Ensuring genetic diversity during directional change in climate (e.g. increasing aridity) requires proactive approaches to conservation and restoration projects. To address these challenges, TERN provides environmental RI at three scales of observation: (i) environmental monitoring using remote sensing techniques at a landscape and continental scale; (ii) a spatially extensive network of ecosystem monitoring plots; and (iii) intensely measured sites collecting detailed data on ecosystem processes. Through partnerships with international environmental RIs, TERN enables research that addresses global challenges, on the first steps toward the forecasting of ecosystem–climate interactions.

**Introduction**

As global climate change becomes more difficult to ignore, there is an urgent need to understand how terrestrial ecosystems can be expected to respond to the changes they experience. Ecosystem responses to climate change and extremes of variability include

increasing drought-induced tree mortality and associated forest dieback (Allen *et al* 2010, Anderegg *et al* 2013, McDowell and Allen 2015), changing distributions of species and loss of habitat (McCallum *et al* 2014, Prober *et al* 2015), rising rates of soil heterotrophic respiration (Bond-Lamberty *et al* 2018), and reductions in primary productivity and soil organic



**Table 1.** List of physical and data research infrastructure (RI) operated by TERN.

RI	Scale	References
Acoustic recorders	P	Karan <i>et al</i> (2016)
Airborne and satellite remote sensing products	L	Held <i>et al</i> (2015)
Biomass <sup>a</sup>	L, P	Karan <i>et al</i> (2016)
Data products and tools	DS	
Flux towers	P	Beringer <i>et al</i> (2016)
Herbaria specimens	S	Tokmakoff <i>et al</i> (2016), Guerin <i>et al</i> (2017)
Leaf area index	S, P	Macfarlane <i>et al</i> (2007a), Macfarlane <i>et al</i> (2007b), Macfarlane <i>et al</i> (2014)
Mangrove floristics	L	
Meteorological and soil sensors	P	Beringer <i>et al</i> (2016)
Permanent plots	S	Tokmakoff <i>et al</i> (2016), Guerin <i>et al</i> (2017)
Phenocams	L, P	Karan <i>et al</i> (2016)
Photopoints	S, P	
Soil and landscape Grid of Australia	L	Grundy <i>et al</i> (2015)
Soil, vegetation and eDNA samples	S	Lemetre <i>et al</i> (2017)
Technical personnel to operate and maintain RI	All	

Note. P: Ecosystem processes; L: Landscapes; S: Ecosystem surveillance; DS: Data services and analytics.

<sup>a</sup> Allometric scaling from field collections of diameter at breast height, basal area, tree height, tree growth via dendrometric records.

matter (Ciais *et al* 2005, Crowther *et al* 2016). However, our understanding of ecosystem responses to climate change and variability has lagged far behind our ability to predict those responses using models. Environmental research infrastructure (RI) is required at national, regional, continental and global scales to address important environmental challenges such as the impacts of climate change, coral bleaching, biodiversity threats, geohazards and extreme events. Establishing a coherent RI across a diverse range of scientific

disciplines and contributing networks is a vital challenge to solve, thus creating a goal for developing cooperation amongst environmental RI organisations, government and industry for the shared purpose of addressing global challenges.

The Terrestrial Ecosystem Research Network (TERN) is Australia's terrestrial ecosystem observatory, providing environmental RI at three scales of observation (table 1 and figure 1): (i) ecosystem surveillance monitoring plots from which spatial

changes in biodiversity are monitored continentally, and temporal changes over long timescales (5–10 years) (Tokmakoff *et al* 2016, Guerin *et al* 2017); (ii) ecosystem processes ‘SuperSites’ equipped with eddy covariance flux towers and from which temporal changes in ecosystem structure and function are monitored at a high level of detail in a spatially limited number of locations (Beringer *et al* 2016, Karan *et al* 2016, van Gorsel *et al* 2018); and (iii) landscapes, spatially distributed soil, environmental monitoring and remote sensing products at continental spatial scales (Grundy *et al* 2015, Mahoney *et al* 2016). TERN provides data infrastructure and analytic services to integrate across the three scales of observation, delivering open access to data publishing (Bissett *et al* 2016, Medeiros and Katz 2016, Lowe *et al* 2017), virtual computing facilities for data users (Guru *et al* 2016) and analysis-code commercialisation (Isaac *et al* 2017). Internationally, environmental RI observatories like TERN are joined together with international partners (e.g. the Strategic Collaboration Council, ILTER, OzFlux, NASA, FLUXNET, NEON, CERN, SAEON, ICOS) to enable research which addresses global challenges like that of ecosystem responses to climate change and variability.

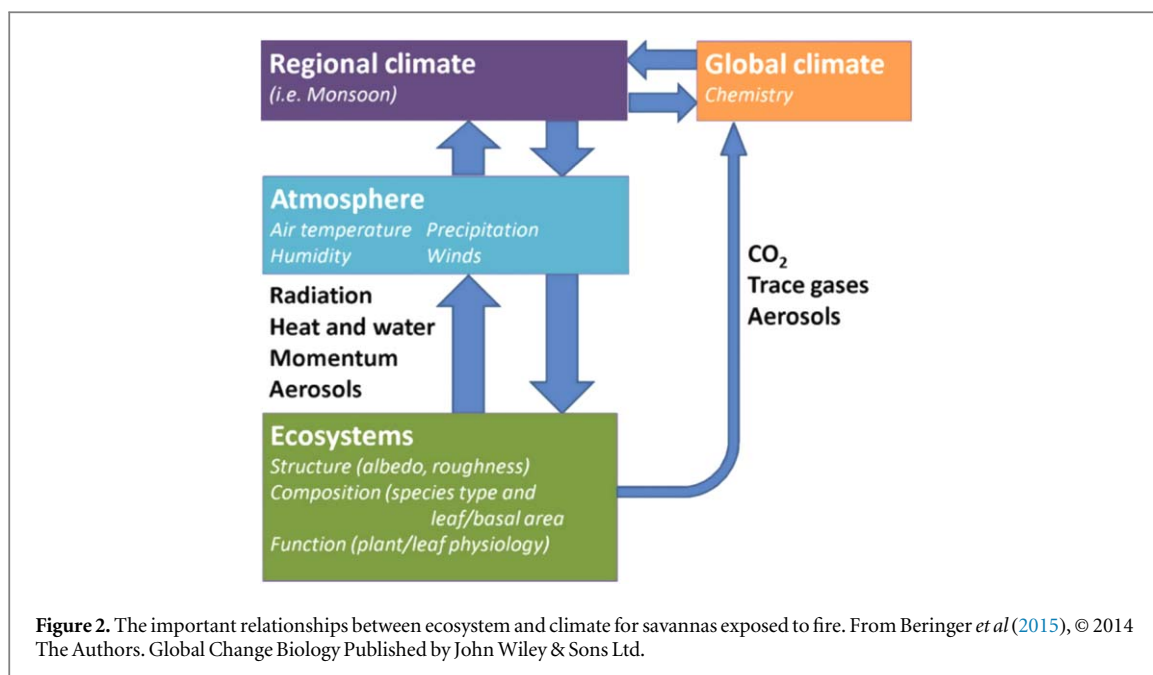
In this letter, we review research across TERN’s scales of observation and through TERN’s international partners for addressing the global challenge of understanding and predicting terrestrial ecosystem responses to climate change and extreme variability. Characteristics of Australia’s sclerophyllous flora point to the ancient development of fire in shaping extensive open ecosystems (>80 Mya; Carpenter *et al* 2015). Development of fire has been associated with increasing aridity, for which the earliest evidence of arid-adapted vegetation appeared more than 30 Mya (Martin 2006). Ecosystem responses to fire and aridity will thus be reviewed first, followed by a review of ecosystem responses to Australia’s highly variable modern climate regime, which was more recently established (during the early Pleistocene, 2 Mya; Martin 2006). Ecosystem responses to climate extremes are further explored for each extreme, presented in sections focused upon (i) an extremely wet period which occurred since TERN’s establishment in 2009 and (ii) the dry extreme, which is associated with drought and heatwave. We will then finish with a section on ecosystem responses to climate change, the most recent of forces to affect ecosystems in Australia and globally. Examples from the literature were obtained upon review of the TERN publications catalogue (<https://tern.org.au/Brochures-Publications-pg27411.html#Publications>). Refer to the supplementary information, available online at [stacks.iop.org/ERL/14/095004/mmedia](https://stacks.iop.org/ERL/14/095004/mmedia) for references from the TERN catalogue which were cited in this letter.

## TERN and global cooperation

TERN was established in 2009 by the Australian government through the National Collaborative Research Infrastructure Strategy (NCRIS) to meet several objectives: to foster scientific interactions in the environmental sciences, to establish a national terrestrial site and observing network, to facilitate access to high-quality environmental data, and to provide a bridge between environmental science and policy (Thurgate *et al* 2017). TERN was originally developed as a network of networks, some of which were established wholly within TERN to fill gaps amongst existing networks (Thurgate *et al* 2017). This combined approach of joining pre-existing and new networks across the environmental space was particularly effective at avoiding duplication (Thurgate *et al* 2017) and thus reducing establishment costs. After expending the capital costs of establishing TERN’s continental RI, the first challenge involved reducing the scope of the RI to fit within the given operations budget whilst retaining a consistent, continental scope. Integration of TERN RI began by extensive consultation which resulted in the grouping of observational infrastructure by scale of measurement, ultimately leading to TERN’s current three scales of observation.

Integration across TERN’s three scales of observation began in the research community (Ma *et al* 2013, Barraza *et al* 2014, Bradford *et al* 2014, Joiner *et al* 2014, Mitchell *et al* 2014, Barraza *et al* 2015, Broich *et al* 2015). Examples of multiscale integration across TERN RI include: through remote-sensing calibration/validation activities (e.g. through NASA SMAP cal/val; Jones *et al* 2017), by informing model parameterisation (Haverd *et al* 2013) and for evaluating model predictability (Haughton *et al* 2018b). With endorsement from the TERN Advisory Board, TERN continues to foster increasingly close integration across three scales of measurement through regular executive group meetings which include programme leaders of RI at each scale of observation and members of TERN’s scientific advisory committee.

As the global research enterprise becomes increasingly interconnected, there is a growing need for internationalising national, regional and continental RI to serve a wider range of researchers as they join forces to tackle global challenges such as climate change, biodiversity loss, food security and infectious diseases. Growing internationalisation is facilitated by interactions with TERN’s international counterparts, which share common objectives, structure and functioning (e.g. NEON, CERN, TERENO, CZO USA). For example, TERN’s flux data are integrated into FLUXNET, a globally distributed environmental RI (Baldocchi *et al* 1996, Gu and Baldocchi 2002, Baldocchi 2008, Novick *et al* 2018) which is improving our understanding of ecosystem responses to fluctuations in environmental conditions (von Buttlar *et al* 2018). In addition, other



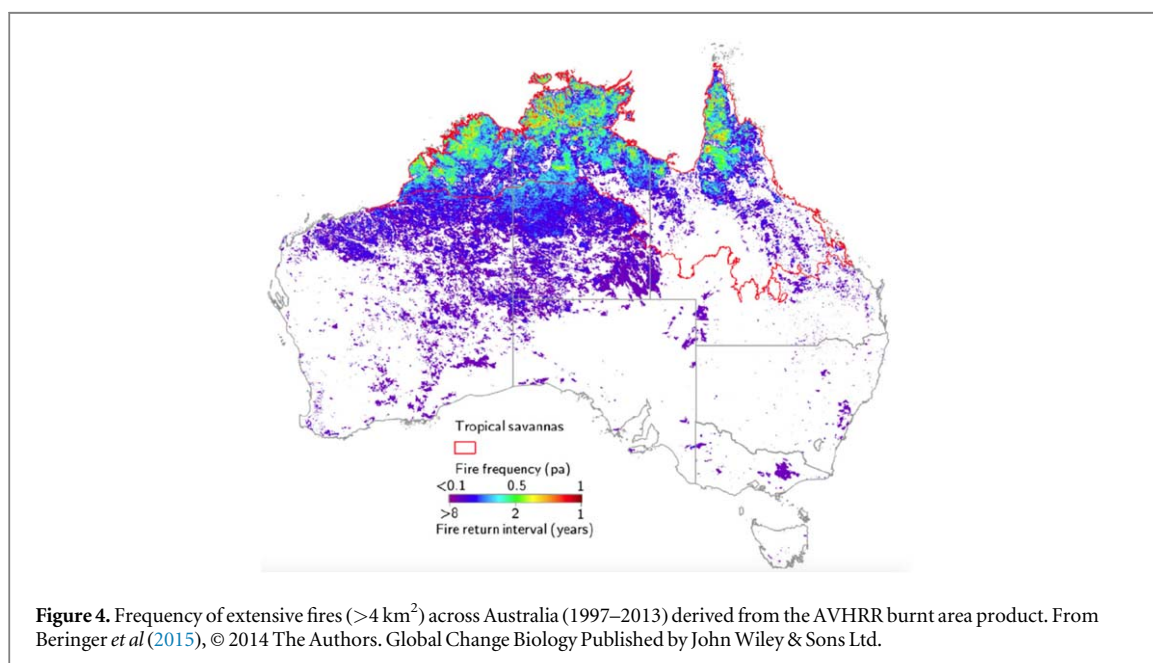
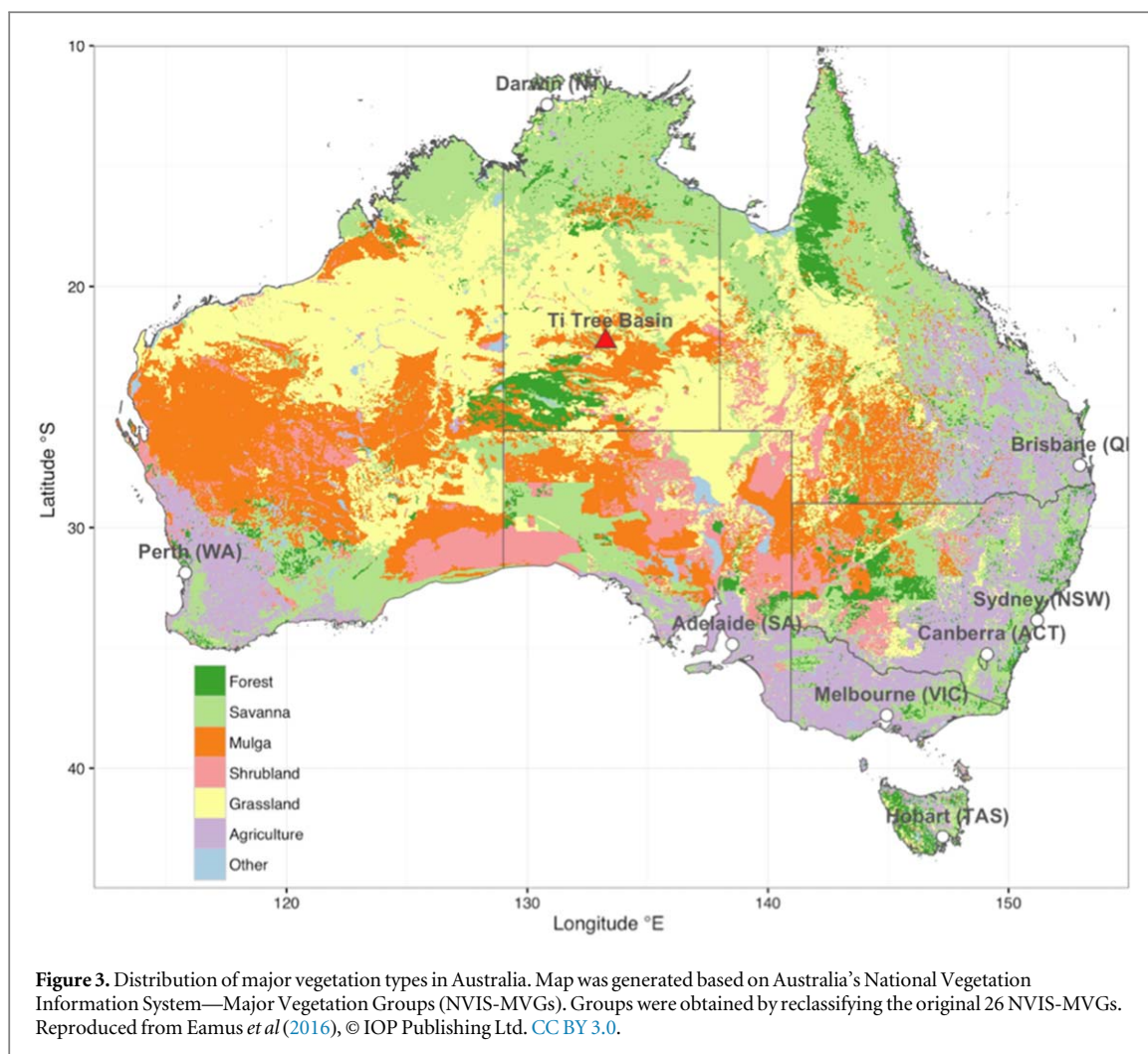
global initiatives and policy frameworks have emerged in recent years to provide global access to data products collected at local or regional scales (e.g. GEOSS, IPBES). In another example of growing internationalisation, the Global Environmental Research Infrastructure (GERI) was formed to foster cooperation amongst RIs by founding members TERN (Australia), SAEON (South Africa), CERN (China), NEON (USA) and eLTER (Europe). TERN is part of an international consortium of environmental RI organisations, with the goal of providing spatially comprehensive and integrated data streams which are model-ready and publicly available for global syntheses. See the supplemental information for further details on TERN's international outreach activities and TERN's twenty-year vision.

### Ecosystems and climate: fire and aridity

An understanding of ecosystem–climate interactions is the foundation of forecasting ecosystem responses to climate change (figure 2; Beringer *et al* 2015), assuming that such predictability is accurate enough to be feasible (Haughton *et al* 2018a). Environmental RI in the form of ecological observatories provides a platform for improved understanding of how ecosystems respond to climate across a diversity of vegetation types. In Australia, 32 major vegetation types have been identified in a national vegetation information system (NVIS; <https://environment.gov.au/land/native-vegetation/national-vegetation-information-system>), although they can be simplified by combining similar types (e.g. arid and semi-arid *Acacia* forests, woodlands, shrublands and savannas are three major vegetation types which are all defined by a dominant canopy of Mulga *Acacia*). By example in a review of key

findings from research using TERN RI at the Alice Mulga SuperSite of the Ti Tree basin, Eamus *et al* (2016) grouped NVIS vegetation types into forest, savanna, Mulga, shrubland, grassland and agriculture (figure 3). Across these landscapes, fire and aridity are key forces shaping ecological relationships with climate.

Bushfire is a primary attribute of the tropical wet-seasonal savannas and semi-arid grasslands of western and northern Australia, where annual fire frequencies are common across the northern tropical savanna (see figures 2 and 4). The concentration of TERN infrastructure in northern Australia at intermediate longitudes is organised around the North Australian Tropical Transect (NATT; figure 1) to support savanna research across a very large precipitation gradient (320 to >1200 mm annual precipitation; Hutley *et al* 2011, Cleverly *et al* 2013, Ma *et al* 2013). Heavy rainfall during the wet season at northernmost locations along the NATT is associated with a large accumulation of biomass (Hutley *et al* 2011), and this grassy biomass cures over the subsequent dry season that lacks rainfall, leading to the very high frequency of fire re-occurrence at the northern end of the NATT (ca. 1–2 years; figure 4). Fire is responsible for the majority of productivity losses in the northern savanna (63%), whereas large weather events such as cyclones contribute very little to the long-term net biome carbon budget (Hutley *et al* 2013). Burning is furthermore largely responsible for greenhouse gas emissions from savannas and consequential greenhouse gas forcing of climate (Bristow *et al* 2016), amongst a cascade of indirect feedbacks between climate and ecosystems which are mediated through local atmospheric dynamics (figure 2; Beringer *et al* 2015). The outcome of this work is that it has contributed to a better understanding of tropical savanna



functioning globally, where similarities of savanna structure have been found to conceal large differences across continents amongst vegetation, climate and fire dynamics (Lehmann *et al* 2014). Without studies of

savanna function such as these which were enabled by TERN RI (and similar RI on other continents), a large gap would exist in the understanding of the differences in savanna function globally.

Outside of the tropics, bushfire tends to follow two patterns. In drylands, fires occur as a result of fuel accumulation directly following the conclusion of very wet periods, whereas in sclerophyllous eucalypt forests, wildfires occur following drought, once fuel has cured sufficiently (Griffin *et al* 1983, Bradstock 2010). At TERN's Calperum Mallee SuperSite (FLUXNET code AU-Cpr) in a Mediterranean climate, bushfire can have little or no effect on soil respiration, but net ecosystem productivity (NEP) and thus gross primary production (GPP) can be reduced following fire (Sun *et al* 2015, 2016, 2017b). Bushfire plays an important role in shaping Australian landscapes, but its observation by environmental RI is limited in time and space, and each event provides a few more hints toward a better understanding of ecosystem responses to fire.

Seventy per cent of Australia is arid or semi-arid (Eamus *et al* 2006), where aridity is likely to dominate over warming and low levels of soil phosphorus in determining adaptation to future climate (Steane *et al* 2017). For example, fauna such as ants, termites and lizards in the Australian tropical savanna are arid-adapted and are thus likely to be resistant to future increases in aridity (Andersen *et al* 2015). By contrast, species in the arid-Mediterranean ecotone are fully adapted to neither climate and are thus sensitive to variations in climate, both spatial and those projected for the future (Guerin *et al* 2016). With aridity increasing globally, international integration of environmental RI organisations create further opportunities for discovering diversity responses to aridity.

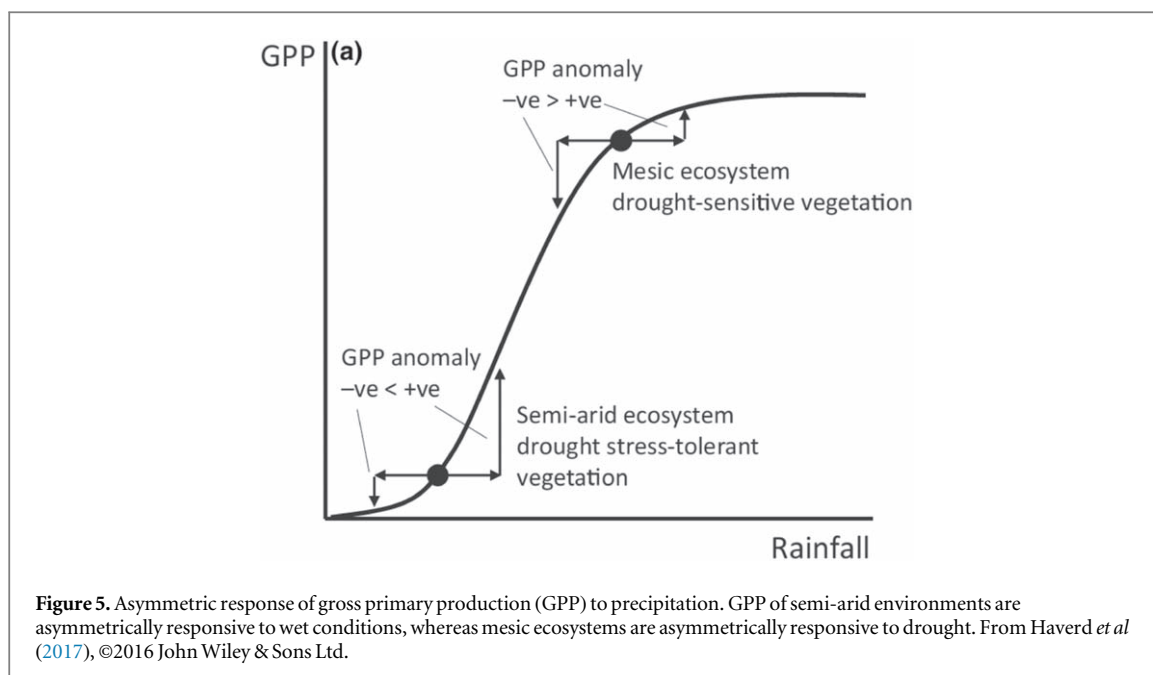
Climate factors associated with aridity include temperature, vapour pressure deficit, solar radiation, precipitation and water availability. Aridity is moreover associated with patterns of water-use efficiency, light-use efficiency, species richness, productivity and adaptability of leaf traits to native growth conditions (Shi *et al* 2014, Gibson *et al* 2017, Rumman *et al* 2018, Bloomfield *et al* 2019). Grasslands are an important and widespread community across the drylands of Australia (figure 3), where climate dynamics are closely related to leaf tissue nutrients (Anderson *et al* 2018). To meet the global challenge of understanding nutrient dynamics in grasslands, TERN is partnered with the Nutrient Network (NutNet) at the Great Western Woodlands SuperSite of southwestern Australia (FLUXNET code AU-GWW, NutNet site Mt. Caroline) (Seabloom *et al* 2015, Firn *et al* 2019). Established to test competing hypotheses for causal mechanisms of relationships between productivity and species richness, initial results from NutNet indicate that climate factors related to aridity such as temperature and the amount and timing of precipitation are positively related to both richness and productivity (Grace *et al* 2016).

## Ecosystems and climate: climate variability and extreme events

Australia's climate is highly variable, with the cultural and economic significance of this highly variable climate illustrated in the well-known common parlance as 'a land ... of droughts and flooding rains' (Dorothea Mackellar, <https://dorotheamackellar.com.au/archive/mycountry.htm>). A full range of vegetation and climate conditions are currently under-sampled by environmental RI globally (Jones *et al* 2017), thus the high temperature anomalies experienced by Australian ecosystems provides the world with an important end-member for developing an understanding of ecosystem responses to climate extremes (e.g. heatwaves; De Kauwe *et al* 2019).

Australia has recently experienced an increase in the frequency and severity of climate extremes (e.g. drought, flooding, heatwave; Cleverly *et al* 2016a, Ellis and Albrecht 2017), and fire has mediated biodiversity responses to this rise in climate extremes in a biome-specific manner (Greenville *et al* 2018). For example, many of the grasslands and savannas of Australia are pyrophytic or 'fire promoting', generating large conflagrations in response to a highly variable climate, either seasonally or episodically (Nicholas *et al* 2011, Beringer *et al* 2015, Wright 2018). By contrast, other vegetation associations like the Mulga (*Acacia* spp.) lands (shrublands, woodlands and savannas) which cover one-fifth of the Australian continent as shown in figure 3 (Bowman *et al* 2008) are sensitive to fire, but they also act as a fire retardant (Murphy *et al* 2010). Instead of burning, these ecosystems show adaptations to extreme climate fluctuations with large variations in water-use efficiency, allowing them to exert control on drainage and recharge which is unaffected by variability in hydroclimate (Chen *et al* 2014, 2016). Across this myriad of different vegetation types and responses to extreme climate variability, adaptation to environmental variability in temperature and water availability in Australia is associated with gene regions (instead of complete genomes) (Christmas *et al* 2016a) and has led to synchronisation of landscape productivity and greenness with hydroclimatic extremes (Cleverly *et al* 2013, Ma *et al* 2015, Rammig and Mahecha 2015).

Ultimately, climate and weather are influenced by ocean-atmosphere interactions within ocean-basin modes of variability. For example, El Niño-Southern Oscillation (ENSO) is driven by a seasonal gradient of sea-surface temperature along the equatorial Pacific Ocean (Trenberth 1997), and fluctuations between the warm phase (El Niño) and the cold phase (La Niña) generally bring contrasting conditions to Northern and Southern Hemispheres. El Niño is associated with maritime wet conditions to the Northern Hemisphere and dry conditions across the Southern Hemisphere, whereas La Niña is associated with reversed



impacts on precipitation and consequently ecosystems (Holmgren *et al* 2001). Data from TERN RI have been used to demonstrate that Australia shows continental phenological responses to ENSO-driven climate variability (Broich *et al* 2015) and that litterfall in the tropical rainforest of northeastern Australia is mainly driven by fluctuations in maximum temperature, which are related to ENSO (Edwards *et al* 2018).

Although ENSO provides the dominant climate signal for global weather patterns, it is becoming apparent that ENSO alone cannot fully explain differences in regional climate variability. Strong coupling amongst the tropical Pacific, Atlantic and Indian Oceans can impact the state of the climate, although limitations still exist in our ability to project future climate without including these teleconnections in climate models (Cai *et al* 2019). In Australia, extreme climate variability (floods, droughts, heatwaves) and resultant effects on water resources have been explained by interactions of the three nearest climate modes: ENSO, the Indian Ocean dipole (IOD) and the Southern annular mode (SAM) in the Southern Ocean (Ummenhofer *et al* 2009, 2011, Perkins *et al* 2015, Xie *et al* 2016, Cleverly *et al* 2016a, Rogers and Beringer 2017).

The relative strength of a particular climate mode depends upon a given continent's location and the relative importance of direct (i.e. baroclinic) or indirect effects (i.e. Rossby-wave propagation) of the surrounding climate modes (Cai *et al* 2011). For example in the northern savanna of Australia, TERN RI was used to show that interannual variability in productivity is associated with climate variability in SOI (Moore *et al* 2018). In southern and central Australia, ENSO, IOD and SAM each contribute to variability in rainfall (He and Guan 2013, He *et al* 2014, Cleverly *et al* 2016a), and as a result of TERN RI, Australian ecosystems have been shown to be very resilient to these high

levels of rainfall variability (Ma *et al* 2016, Cleverly *et al* 2016b, 2016c).

### Wet extremes: flooding rain

The two wettest events on record in Australia occurred in 1973–1976 and 2010–2012, both bringing widespread flooding nationally (Meyer *et al* 2015, Cleverly *et al* 2016a, 2016b, Whelan and Frederiksen 2017). In this letter, we focus on the more recent event, which overlapped with the establishment of TERN. Augmentation of precipitation in the Southern Hemisphere during this very strong La Niña was so large that ocean levels reversed their long-term trend and dropped by 5 mm (Boening *et al* 2012, Fasullo *et al* 2013). As a result, much of Australia's dryland flushed with greenness in satellite retrievals of both the normalised difference vegetation index and the enhanced vegetation index (Wardle *et al* 2013, Cleverly *et al* 2016a), leading to several ecological responses. Plagues of rats emerge during wet extremes which are absent during dry times (Greenville *et al* 2013). Masting occurred in dryland plants, with reproductive structures increasing in mass 300%–7000% during 2010–2012 (Travers and Eldridge 2013). An ecosystem-wide compositional shift occurred in the Simpson Desert, with rooting patterns and soil texture explaining phenological timing and distribution of each plant form (annual grasses and forbs, perennial grasses, shrubs; Nano and Pavey 2013). Wet extremes have the potential to transform the ecology of vast portions of Australia.

Increased water availability resulted in an asymmetrically large increase in CO<sub>2</sub> uptake by semi-arid and temperate regions of Australia, Africa, South America and India (figure 5; Haverd *et al* 2017), with



the majority of this global land C sink anomaly located in Australia (Poulter *et al* 2014). Carbon fluxes and phenology measured by TERN's RI in semi-arid and Mediterranean climates of Australia confirmed the continent's role in the 2011 global land C sink anomaly (Cleverly *et al* 2013, Eamus *et al* 2013b, Ma *et al* 2015, Sun *et al* 2018). Photosynthesis and respiration are limited by water availability across much of Australia, with both responding positively to extreme precipitation (Cleverly *et al* 2013, Haverd *et al* 2016) and thus maintaining relatively small NEP and reduced carbon-use efficiency (i.e. NEP/GPP) during wet extremes. Low carbon-use efficiency during wet conditions and water limitations on soil respiration during subsequent dry periods contribute to minimisation of carbon emissions after the conclusion of the wet extreme, in the absence of abiotic decomposition (Cleverly *et al* 2013, 2016c).

Multiple aspects of the climate contributed equally to increased CO<sub>2</sub> uptake in Australia (Trudinger *et al* 2016), showing the 2011 global land C sink anomaly to be an integrated climatological, meteorological and ecosystem event (Cleverly *et al* 2016a). However, there were two restrictions on Australia's contribution to the land C sink anomaly. First, the asymmetric response of photosynthetic productivity to precipitation is dependent upon antecedent conditions, either amplifying or dampening their relationship (Sun *et al* 2017a). The land C sink anomaly followed the driest and hottest year of the Millennium Drought, thus antecedent water resources were at a minimum (van Dijk *et al* 2013). Second, energy-limited ecosystems did not show a similar asymmetric response to extrinsic forcing by precipitation and thus did not respond to climate forcing during the land C sink anomaly in the same way that semi-arid ecosystems did (figure 5, Haverd *et al* 2017). Thus, the contribution of enhanced productivity in coastal, energy-limited ecosystems was expected to be small, whereas Australia's vast drylands have a high capacity for enhanced productivity during wet extremes (figure 5). Even with these limitations, the land C sink provided an ecosystem service which might have helped to slow the rate of climate change (Keenan and Williams 2018).

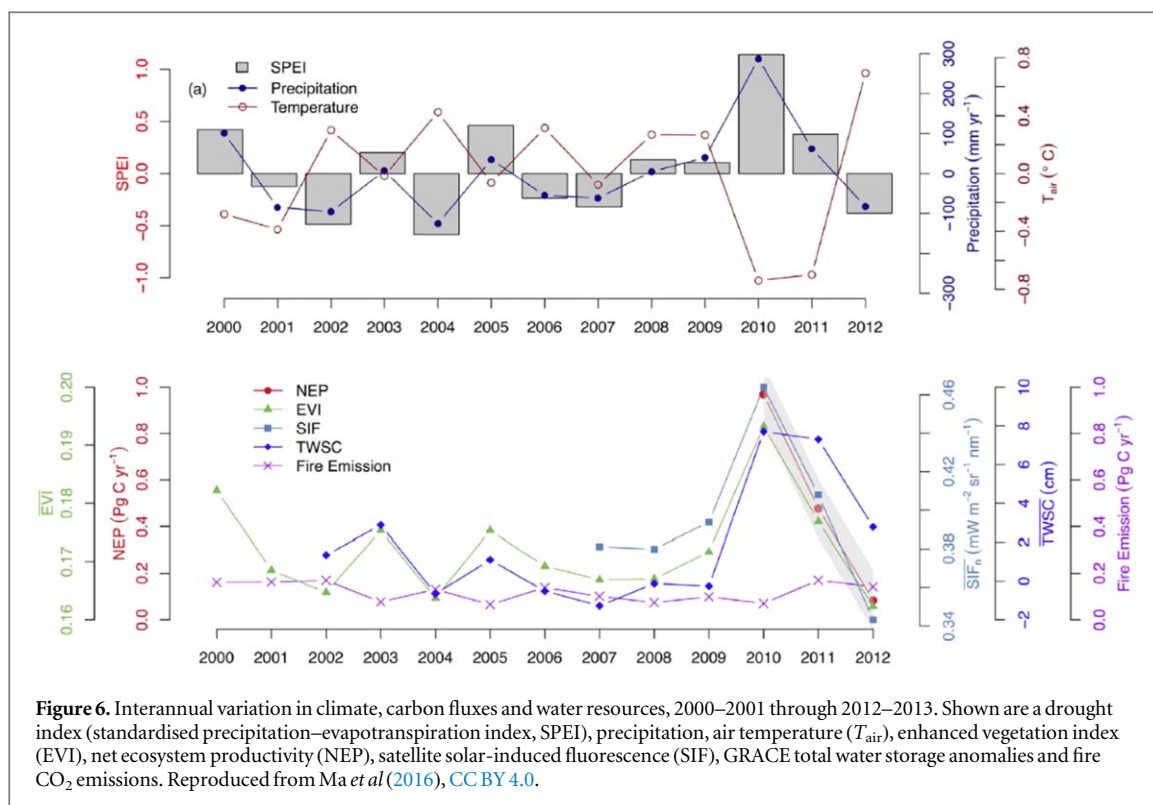
An inevitable outcome of increased productivity is biomass accumulation, especially across grasslands globally, where biomass accumulation is related to climate variability (Morgan *et al* 2016). Reduced diversity can result with the presence of a single species of invasive grass (e.g. buffel grass, *Cenchrus ciliaris*), which burns hotter and more completely than native grasses (Schlesinger *et al* 2013). For hummock grasslands which cover one-quarter of the Australian land area (Bowman *et al* 2008), the legacy of biomass accumulated during the 2011 land C sink anomaly persisted in the absence of burning for years as a strong carbon source due to photodegradation of the standing leaf litter (Cleverly *et al* 2016c). C budgets like those of hummock grasslands are very difficult to predict using

land surface models (Haughton *et al* 2018a) due to a lack of theoretical foundation for the modelling of abiotic decomposition. This is thus an active area of research for which TERN's environmental RI will play an important role in integrating measurements, monitoring, modelling and remote sensing of carbon and water balances (Eamus *et al* 2016).

### Dry extremes: drought and heatwave

Interannual variability in the global carbon cycle is strongly related to the large variability of the semi-arid land C sink (Ahlström *et al* 2015). In a single example, the 2011 land C sink in Australia was immediately followed by the return of drought and associated heat, which shut down the Australian land C sink even whilst total water storage on the continent had persisted (figure 6; Fasullo *et al* 2013, Ma *et al* 2016). Thus, photosynthetic productivity of Australia is sensitive to meteorological drought (i.e. months to years of below-normal precipitation) and agricultural drought (i.e. yield reduction due to soil drying), but Australia's hydroclimatic variability can moderate against a more severe hydrological drought (i.e. decline of water storage below the long-term mean; figure 6; Dai 2011). Even during long-term drought, moderately wetter-than-average years can have a strong positive effect on total water storage and productivity across Australia (figure 6). The Millennium Drought of 2001–2009 was the longest meteorological drought on record in Australia, but antecedent hydrological drought began in 1994 (van Dijk *et al* 2013). During the Millennium Drought, a worldwide reduction in photosynthetic productivity was attributed to drying in the Southern Hemisphere (Zhao and Running 2010). Despite a widespread and severe reduction in CO<sub>2</sub> uptake during the Millennium Drought, Australian vegetation has shown resilience to a drought as extreme as even it was (figure 6; Campos *et al* 2013, Ma *et al* 2013, 2015).

Australia has experienced much dryer, longer droughts during previous glacial maxima (Martin 2006), and this long history of drought has conferred a level of adaptation in Australia's vegetation. At the mesic end of the aridity gradient, the structure of tropical rainforest trees is adapted to the maximum historical water deficit (Pfeifer *et al* 2018). In the more arid-adapted Mallee, a multi-stemmed eucalypt which is also fire adapted, survival of common dry periods is achieved by maintaining conservative (i.e. very small) rates of transpiration (Meyer *et al* 2015). Two sequential years of much below-average precipitation in central Australia (mid-2011–2013) resulted in a shift from a strong carbon sink to a carbon source, whilst showing resilience during the subsequent return of average annual precipitation amounts (Cleverly *et al* 2016b, 2016c). Australian ecosystems show a diversity of hydraulic traits, the presence of which confers



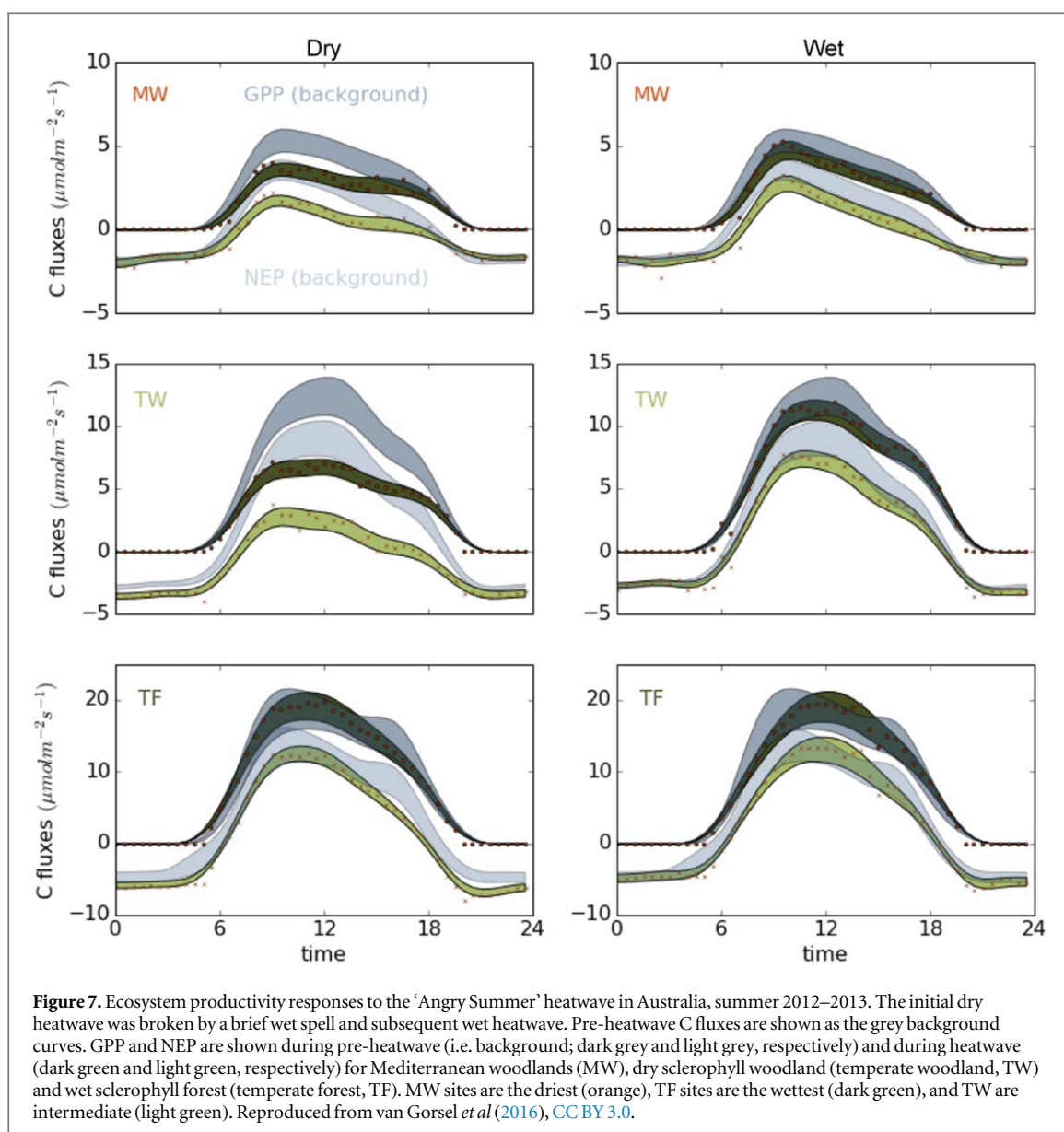
resilience to water stress (Nolan *et al* 2017, Anderegg *et al* 2018).

Heatwaves have been increasing in frequency worldwide over the last 20–50 years, and they have been either combined with drought or have occurred under wet conditions, although heatwaves are more commonly associated with drought (Ding and Qian 2011, Bastos *et al* 2014, Teskey *et al* 2015, Kang and Eltahir 2018). Three characteristics of heatwaves, their frequency, intensity and duration, are projected to continue increasing through the end of the 21st century (Perkins-Kirkpatrick *et al* 2016). For example, the drought and heatwave which struck Europe in 2003 was so severe and so far outside of the historical record that the return interval estimates are in the range of thousands to millions of years (Schar *et al* 2004), but another similar heatwave is expected to occur within the next 30 years (Russo *et al* 2015). The combination of heatwave and drought, also known as global change-type drought, can have consequences on ecosystems as severe as tree mortality and forest dieback (Breshears *et al* 2009, Eamus *et al* 2013a), and the likelihood of mortality is expected to increase as the frequency, intensity and duration of heatwaves increases.

Soil-moisture–temperature and soil-moisture–precipitation feedbacks are important for development and maintenance of Australian heatwaves, albeit not as important as these mechanisms are for European heatwaves (Perkins *et al* 2015). Drier-than-average conditions in Australia’s interior push hot, dry winds into southern Australia from The North (Griebel *et al* 2016). One Australian example was the 2012/2013 ‘Angry Summer’ heatwave, which developed

as drought across the interior of the continent, and an associated high-pressure ridge pushed high temperatures into forests and woodlands of southern Australia (van Gorsel *et al* 2016, Cleverly *et al* 2016c).

Ecosystem functional responses to both phases of the ‘Angry Summer’ heatwave (dry followed by wet) were evaluated using TERN’s flux tower infrastructure at seven TERN ecosystem processes sites across southern Australia (van Gorsel *et al* 2016). NEP and GPP declined sharply during the heatwave in Mediterranean woodlands and dry sclerophyll forests, although reductions were smaller during the wet phase than during the preceding dry phase (figure 7). By contrast, the wet sclerophyll forest at the Tumberumba Super-Site maintained NEP and GPP at constant levels as before the heatwave, with evaporative cooling ameliorating the heatwave and weakening land–atmosphere feedbacks (figure 7; van Gorsel *et al* 2016). However, soil moisture reserves were nearly depleted in the wet sclerophyll forest during the relatively short ‘Angry Summer’ heatwave, showing afternoon reductions of NEP and GPP during the dry portion of the heatwave, which is consistent with a photosynthetic and stomatal down-regulation due to stress (see figure 7, Cowan and Farquhar 1977). Thus, this heatwave provided a second example of the associated effects of drought and heatwave on ecosystem productivity of Australian ecosystems (see figures 6 and 7) and further demonstrates that increases in the intensity, frequency or duration of heatwaves in future might have seriously detrimental consequences for even Australia’s wettest forests (van Gorsel *et al* 2016).

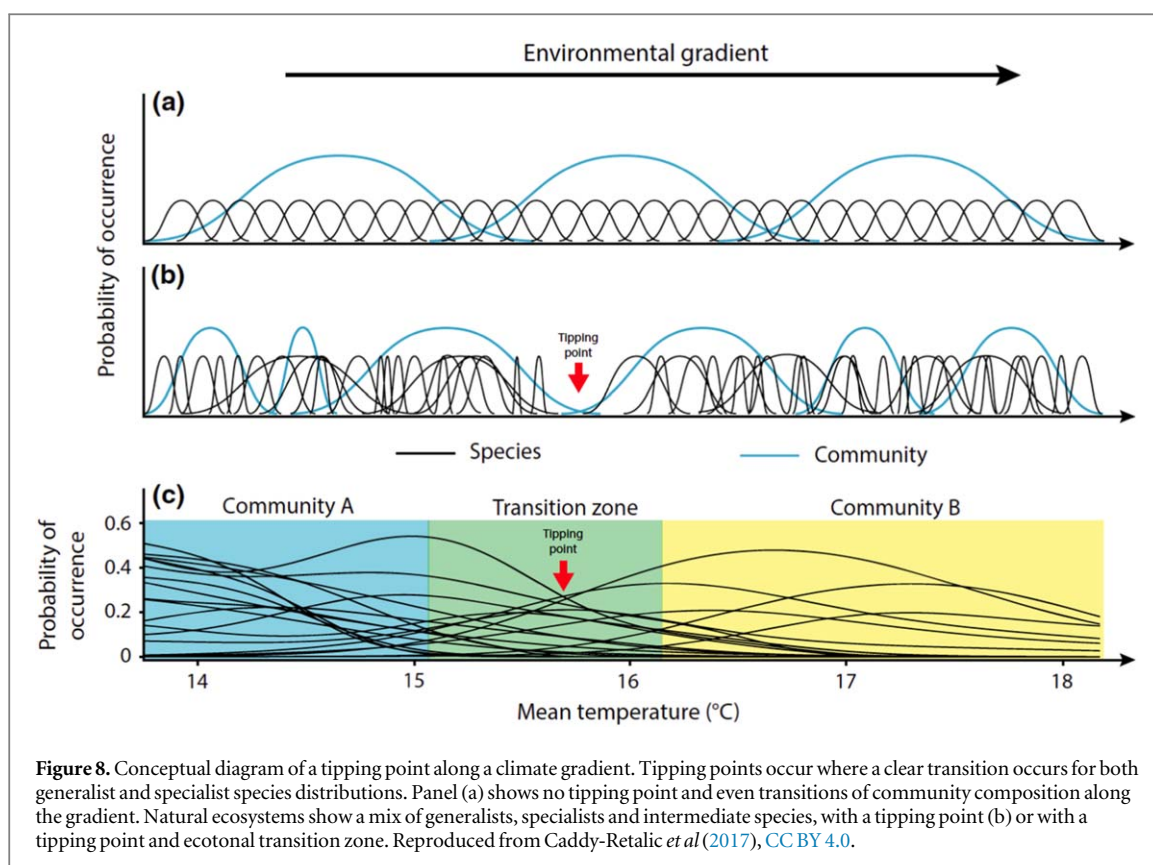


## Ecosystems and climate: climate change

Ecosystems can be vulnerable to climate change due to restricted gene flow, habitat loss or restricted range (McCallum *et al* 2014). However, cool and mesic locations in the landscape can often provide refugia where higher resilience is encountered than would be otherwise predicted (Guerin *et al* 2013, Tapper *et al* 2014, Christmas *et al* 2017). Refugia on mountains and islands can buffer genetic diversity against a fluctuating climate (Christmas *et al* 2017), although climate change can remain a threat for isolated ecosystems such as for island cloud forests where decreasing precipitation and cloud cover have been observed (Auld and Leishman 2015). Furthermore, refugia can show a tipping point, described as a point in a spatial climate gradient at which ecosystem composition turns over rapidly (figure 8; Guerin *et al* 2013, Caddy-Retalic *et al* 2017). Tipping points occur at locations along an environmental climate gradient where the

species composition of both generalists and specialists changes (figure 8). Such a transition zone would exist at the boundary of a climate refugium, where a turnover of multiple species occurs over a short distance (figure 8). The presence of a tipping point carries a further risk from climate change as the locations of tipping points contract toward the centre of a species’ range. Long-term ecological RI from various countries worldwide, including Australia, has been joined into the International Long Term Ecological Network (ILTER), which addresses the grand challenge of climate change and the resultant loss of biodiversity which is likely to occur (Mirtl *et al* 2018).

Thus far, we have discussed how adaptation, such as adaptation to aridity, can play an important role in protecting biodiversity from climate extremes, but considerations of adaptation and adaptability are also important for biodiversity conservation in a changing climate. Care must be taken, however, to avoid deprioritising refugia which are low in diversity and



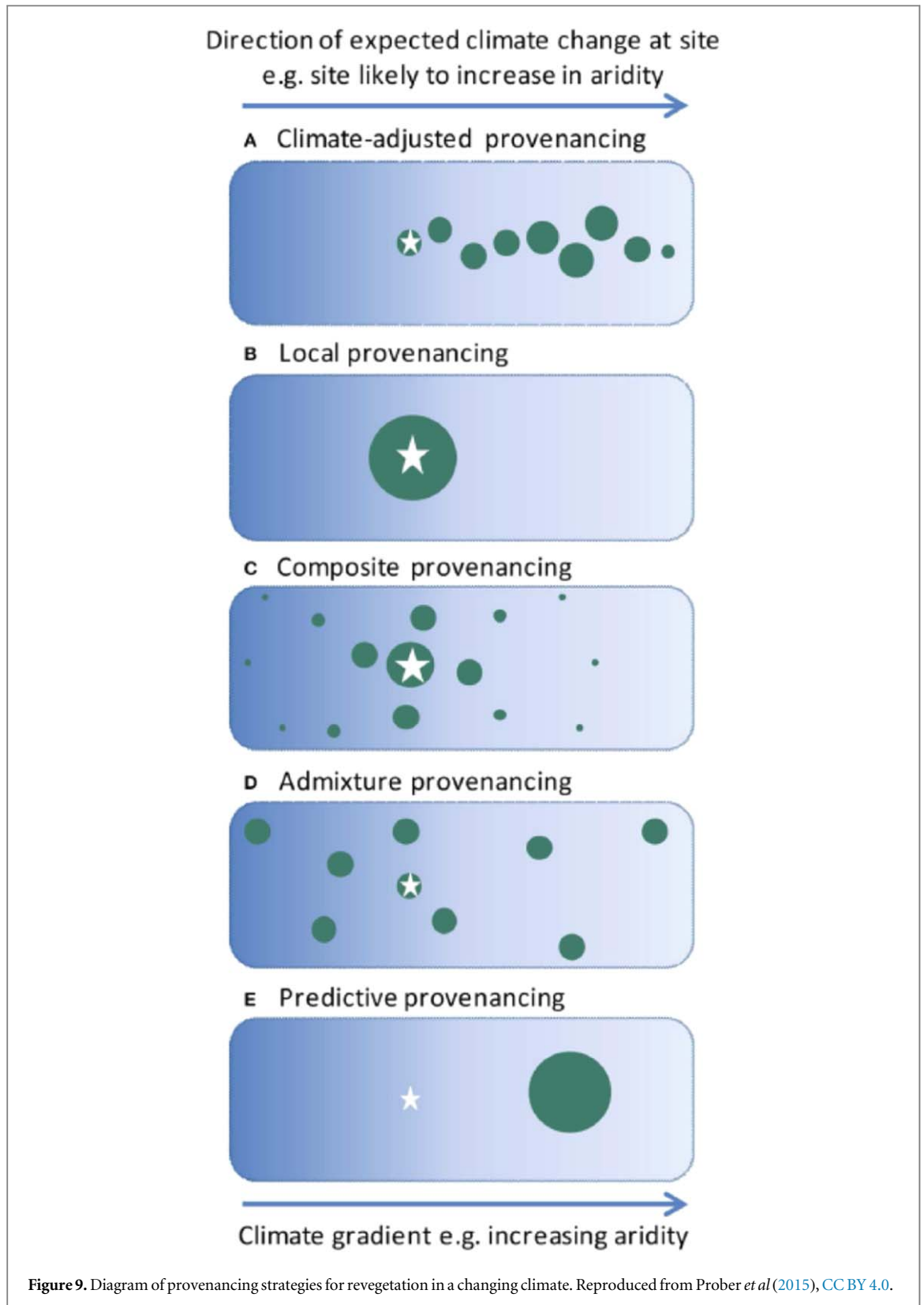
**Figure 8.** Conceptual diagram of a tipping point along a climate gradient. Tipping points occur where a clear transition occurs for both generalist and specialist species distributions. Panel (a) shows no tipping point and even transitions of community composition along the gradient. Natural ecosystems show a mix of generalists, specialists and intermediate species, with a tipping point (b) or with a tipping point and ecotonal transition zone. Reproduced from Caddy-Retalic *et al* (2017), CC BY 4.0.

thereby less adapted to areas outside of their refugium (Costion *et al* 2015). Otherwise, several conservation approaches are available for promoting diversity and adaptability to climate change, including climate-adjusted provenancing (figure 9), assisted migration, biodiversity corridors and *ex situ* strategies (Prober *et al* 2015, Christmas *et al* 2016b). In climate-adjusted provenancing, natural genetic variability is exploited to enhance climate resilience of restoration activities over time by predicting future changes in climate over incremental time steps (figure 9). This gradual approach over time allows for the detection of uncertainties (e.g. mismatch between predicted and actual climate change trajectories) before it is too late to correct for them (figure 9). TERN's plot-based monitoring infrastructure, especially those arrayed in transects along climate gradients, provide a powerful tool for evaluating community responses to climate change and for promoting resilience in biodiversity (Caddy-Retalic *et al* 2017).

There are several aspects of projected climate change in relation to ecosystem carbon cycles, such as changes in precipitation, vapour pressure deficit, temperature and elevated  $[\text{CO}_2]$ . Changes in precipitation seasonality are projected to reduce carbon stocks in the northern Australian savannas and rainforests, even with little change to annual total precipitation (Cook *et al* 2015). Increasing vapour pressure deficit during one key season as a result of decreasing seasonal precipitation and increasing temperature is expected to carry detrimental effects

upon the carbon cycle of Australian alpine grasslands and tropical rainforests worldwide (Fu *et al* 2018, Marchin *et al* 2018). Photosynthetic production in tropical rainforests is currently restricted by high vapour pressure deficit, and they are unlikely to tolerate a much drier atmosphere (Fu *et al* 2018). In alpine grasslands of Australia, a tipping point has been identified wherein vapour pressure deficits which exceed this threshold can prevent the typical recovery of vegetational greenness at the end of the growing season (Marchin *et al* 2018). Increasingly elevated vapour pressure deficit is a serious risk for tree mortality and ecosystem function worldwide (Allen *et al* 2010, Breshears *et al* 2013, Eamus *et al* 2013a).

Warming is predicted to have strongly negative effects on Australia's temperate eucalypt forests, nearly 90% of which exist in temperature regimes above their thermal optimum for growth (11 °C; Bowman *et al* 2014). In the absence of water or substrate limitations, respiration will increase along with rising temperatures, leading to global observations of increasing heterotrophic respiration and climate-driven loss of soil carbon (Bond-Lamberty *et al* 2018). Acting to counter the effects of increasing temperature, elevated  $[\text{CO}_2]$  can contribute to maintenance of photosynthesis at reduced stomatal conductance, thereby improving water-use efficiency whilst reducing pressure on limited water resources.  $\text{CO}_2$  fertilisation is projected to be the main driver of savanna responses to climate, leading to increased carbon sequestration in vegetation, although the magnitude



**Figure 9.** Diagram of provenancing strategies for revegetation in a changing climate. Reproduced from Prober *et al* (2015), CC BY 4.0.

of the fertilisation effect will depend strongly upon changes in fire return interval and seasonality (Scheiter *et al* 2015). Increasing aridity and elevated  $[\text{CO}_2]$  are likely to affect vegetation dynamics of tropical savannas, which will alter fire regimes and provide further carbon feedbacks to climate (figure 2; Beringer *et al* 2015).

### Final remarks

There is an urgent need for environmental information from RI in remote Australian landscapes, which would provide important outcomes and impact related to environmental reporting and fostering research in the framework of global challenges

(van Dijk *et al* 2014). The risks of climate change as well as opportunities for conservation are emerging from this work, although there is still much to discover. Environmental RIs create the opportunity for identifying and evaluating the key drivers of ecosystem change by allowing researchers to observe state-changing events such as heatwaves, floods or droughts in locations which might be otherwise inaccessible. These are the first steps toward the development of an environmental forecasting system which can answer the global challenge of predicting ecosystem responses to climate change.

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## Data availability statement

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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