TERN, Australia's Land Observatory: addressing the global challenge of forecasting ecosystem responses to climate variability and change

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1   TERN, Australia's Land Observatory: addressing the global challenge of forecasting
2   ecosystem responses to climate variability and change

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27   9326/page/Environmental-Research-Infrastructures)

28   **Abstract**

29   The global challenge of understanding and forecasting ecosystem responses to climate

30   extremes and climate change is addressed in this review of research enabled through

31   environmental research infrastructure (RI) provided by Australia's Terrestrial Ecosystem

32   Research Network (TERN). Two primary climatic drivers of ecosystem structure and

33   function in Australia are fire and aridity, to which Australian flora and fauna has shown

34   marked adaptability. Australian vegetation shows resilience to climate extremes of flooding

35   rains, droughts and heatwaves such that variability in primary productivity of Australian

36   vegetation has a tangible effect on the global carbon cycle. Nonetheless, Australian flora and

37   ecosystems could be vulnerable to projected climate change (e.g., to increasing vapour

38   pressure deficit). Refugia are also vulnerable to climate change, with conditions in these

39   areas already near the tipping point for a change in community composition. Ensuring

40   genetic diversity during directional change in climate (e.g., increasing aridity) requires

41   proactive approaches to conservation and restoration projects. To address these challenges,

42   TERN provides environmental research infrastructure (RI) at three scales of observation: i)

43   environmental monitoring using remote sensing techniques at a landscape and continental

44   scale; ii) a spatially extensive network of ecosystem monitoring plots; and iii) intensely

45   measured sites collecting detailed data on ecosystem processes. Through partnerships with

46   international environmental RIs, TERN enables research that addresses global challenges, on

47   the first steps toward the forecasting of ecosystem–climate interactions.

48   **Keywords**

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3   **Introduction**
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6   51   As global climate change becomes more difficult to ignore, there is an urgent need to
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8   53   understand how terrestrial ecosystems can be expected to respond to the changes they
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10   54   experience. Ecosystem responses to climate change and extremes of variability include
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12   55   increasing drought-induced tree mortality and associated forest dieback (Allen *et al.*, 2010;
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14   56   Anderegg *et al.*, 2013; McDowell and Allen, 2015), changing distributions of species and
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16   57   loss of habitat (McCallum *et al.*, 2014; Prober *et al.*, 2015), rising rates of soil heterotrophic
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18   58   respiration (Bond-Lamberty *et al.*, 2018), and reductions in primary productivity and soil
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20   59   organic matter (Ciais *et al.*, 2005; Crowther *et al.*, 2016). However, our understanding of
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22   60   ecosystem responses to climate change and variability has lagged far behind our ability to
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24   61   predict those responses using models. Environmental research infrastructure (RI) is required
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26   62   at national, regional, continental and global scales to address important environmental
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28   63   challenges such as the impacts of climate change, coral bleaching, biodiversity threats,
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30   64   geohazards and extreme events. Establishing a coherent RI across a diverse range of
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32   65   scientific disciplines and contributing networks is a vital challenge to solve, thus creating a
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34   66   goal for developing cooperation amongst environmental RI organisations, government and
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36   67   industry for the shared purpose of addressing global challenges.
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38   68   The Terrestrial Ecosystem Research Network (TERN) is Australia's terrestrial ecosystem
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40   69   observatory, providing environmental RI at three scales of observation (Table 1 and Fig. 1):
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42   70   (i) ecosystem surveillance monitoring plots from which spatial changes in biodiversity are
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44   71   monitored continentally, and temporal changes over long timescales (5–10 years)
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46   72   (Tokmakoff *et al.*, 2016; Guerin *et al.*, 2017); (ii) ecosystem processes 'SuperSites' equipped
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48   73   with eddy covariance flux towers and from which temporal changes in ecosystem structure
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50   74   and function are monitored at a high level of detail in a spatially limited number of locations
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52   75   (Beringer *et al.*, 2016; Karan *et al.*, 2016; van Gorsel *et al.*, 2018); and (iii) landscapes,

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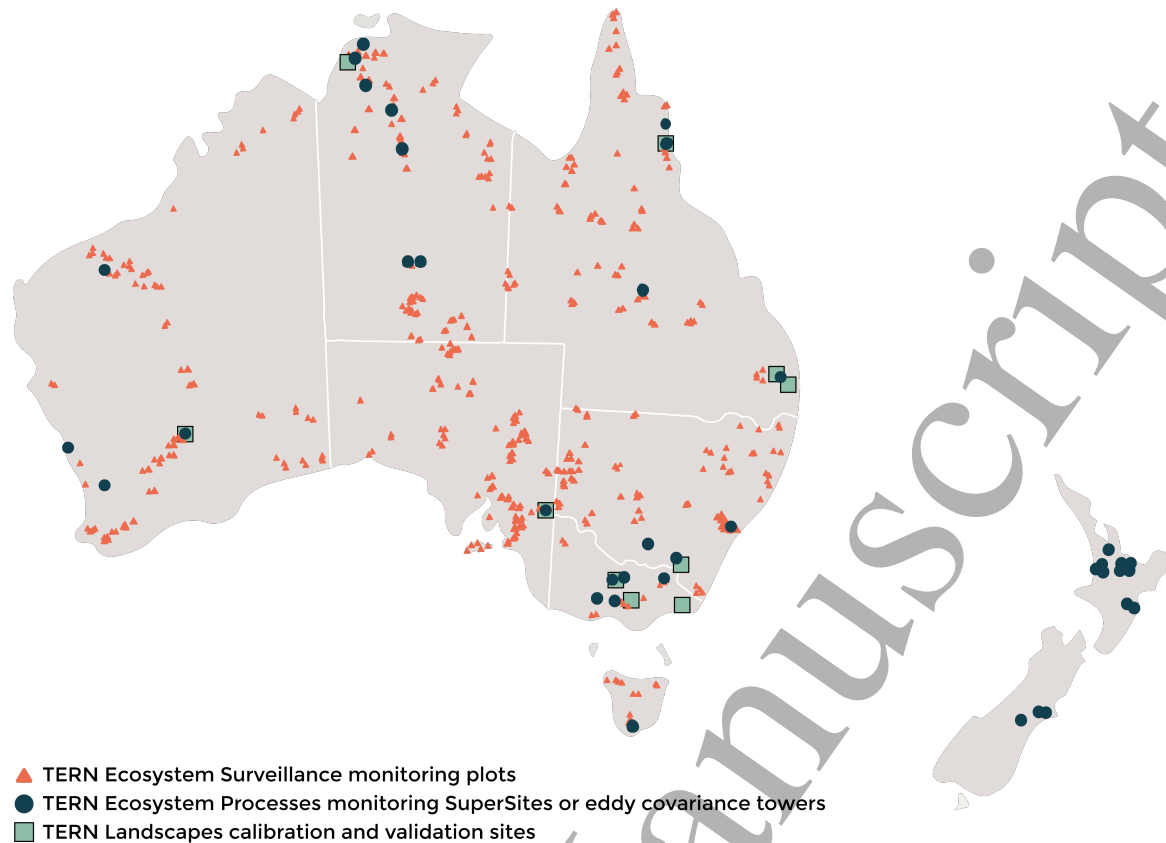
Figure 1. Map of TERN infrastructure including flux towers in New Zealand as part of TERN Oz-Flux. © 2019 TERN at the University of Queensland, used by permission.

76 spatially distributed soil, environmental monitoring and remote sensing products at

77 continental spatial scales (Grundy *et al.*, 2015; Mahoney *et al.*, 2016). TERN provides data

78 infrastructure and analytic services to integrate across the three scales of observation,

79 delivering open access to data publishing (Bissett *et al.*, 2016; Medeiros and Katz, 2016;

80 Lowe *et al.*, 2017), virtual computing facilities for data users (Guru *et al.*, 2016) and analysis-

81 code commercialisation (Isaac *et al.*, 2017). Internationally, environmental RI observatories

82 like TERN are joined together with international partners (e.g., the Strategic Collaboration

83 Council, ILTER, OzFlux, NASA, FLUXNET, NEON, CERN, SAEON, ICOS) to enable

84 research which addresses global challenges like that of ecosystem responses to climate

85 change and variability.

86   In this letter, we review research across TERN's scales of observation and through

87 TERN's international partners for addressing the global challenge of understanding and

88   predicting terrestrial ecosystem responses to climate change and extreme variability.

89   Characteristics of Australia's sclerophyllous flora point to the ancient development of fire in

90   shaping extensive open ecosystems (> 80 Mya; Carpenter *et al.*, 2015). Development of fire

91   has been associated with increasing aridity, for which the earliest evidence of arid-adapted

92   vegetation appeared more than 30 Mya (Martin, 2006). Ecosystem responses to fire and

93   aridity will thus be reviewed first, followed by a review of ecosystem responses to Australia's

94   highly variable modern climate regime, which was more recently established (during the

95   early Pleistocene, 2 Mya; Martin, 2006). Ecosystem responses to climate extremes are

96   further explored for each extreme, presented in sections focused upon (i) an extremely wet

97   period which occurred since TERN's establishment in 2009 and (ii) the dry extreme, which is

98   associated with drought and heatwave. We will then finish with a section on ecosystem

99   responses to climate change, the most recent of forces to affect ecosystems in Australia and

100   globally. Examples from the literature were obtained upon review of the TERN publications

101   catalogue (https://www.tern.org.au/Brochures-Publications-pg27411.html#Publications).

102   Refer to the Supplementary Information for references from the TERN catalogue which were

103   cited in this letter.

TERN and global cooperation

105   TERN was established in 2009 by the Australian government through the National

106   Collaborative Research Infrastructure Strategy (NCRIS) to meet several objectives: to foster

107   scientific interactions in the environmental sciences, to establish a national terrestrial site and

108   observing network, to facilitate access to high-quality environmental data, and to provide a

109   bridge between environmental science and policy (Thurgate *et al.*, 2017). TERN was

110   originally developed as a network of networks, some of which were established wholly

111   within TERN to fill gaps amongst existing networks (Thurgate *et al.*, 2017). This combined

112   approach of joining pre-existing and new networks across the environmental space was

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Table 1. List of physical and data research infrastructure (RI) operated by TERN. P: Ecosystem processes; L: Landscapes; S: Ecosystem surveillance; DS: Data services and analytics.

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

[a] Allometric scaling from field collections of diameter at breast height, basal area, tree height, tree growth via dendrometric records

113 particularly effective at avoiding duplication (Thurgate *et al.*, 2017) and thus reducing

114 establishment costs. After expending the capital costs of establishing TERN's continental RI,

115 the first challenge involved reducing the scope of the RI to fit within the given operations

116 budget whilst retaining a consistent, continental scope. Integration of TERN RI began by

117 extensive consultation which resulted in the grouping of observational infrastructure by scale

118 of measurement, ultimately leading to TERN's current three scales of observation.

119 Integration across TERN's three scales of observation began in the research community

120 (Ma *et al.*, 2013; Barraza *et al.*, 2014; Bradford *et al.*, 2014; Joiner *et al.*, 2014; Mitchell *et*

121 *al.*, 2014; Barraza *et al.*, 2015; Broich *et al.*, 2015). Examples of multiscale integration

122 across TERN RI include: through remote-sensing calibration/validation activities (e.g.,

123 through NASA SMAP cal/val; Jones *et al.*, 2017), by informing model parameterisation

124 (Haverd *et al.*, 2013) and for evaluating model predictability (Haughton *et al.*, 2018b). With

125 endorsement from the TERN Advisory Board, TERN continues to foster increasingly close

126 integration across three scales of measurement through regular executive group meetings

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127 which include program leaders of RI at each scale of observation and members of TERN's

128 scientific advisory committee.

129   As the global research enterprise becomes increasingly interconnected, there is a

130 growing need for internationalising national, regional and continental RI to serve a wider

131 range of researchers as they join forces to tackle global challenges such as climate change,

132 biodiversity loss, food security and infectious diseases. Growing internationalisation is

133 facilitated by interactions with TERN's international counterparts, which share common

134 objectives, structure and functioning (e.g., NEON, CERN, TERENO, CZO USA). For

135 example, TERN's flux data are integrated into FLUXNET, a globally distributed

136 environmental RI (Baldocchi *et al.*, 1996; Gu and Baldocchi, 2002; Baldocchi, 2008; Novick

137 *et al.*, 2018) which is improving our understanding of ecosystem responses to fluctuations in

138 environmental conditions (von Buttlar *et al.*, 2018). In addition, other global initiatives and

139 policy frameworks have emerged in recent years to provide global access to data products

140 collected at local or regional scales (e.g., GEOSS, IPBES). In another example of growing

141 internationalisation, the Global Environmental Research Infrastructure (GERI) was formed to

142 foster cooperation amongst RIs by founding members TERN (Australia), SAEON (South

143 Africa), CERN (China), NEON (USA) and eLTER (Europe). TERN is part of an

144 international consortium of environmental RI organisations, with the goal of providing

145 spatially comprehensive and integrated data streams which are model-ready and publicly

146 available for global syntheses. See the supplemental information for further details on

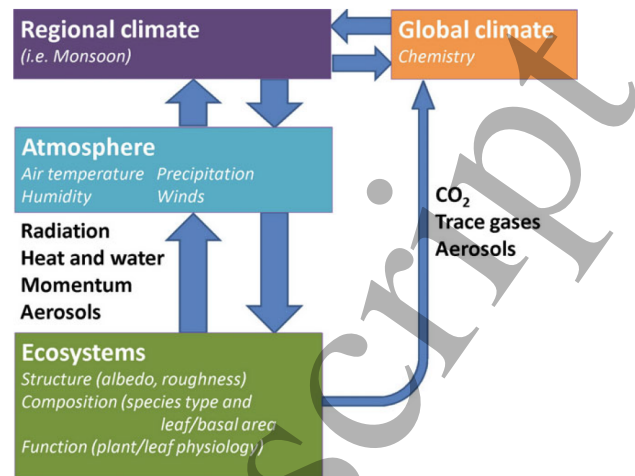147 TERN's international outreach activities and TERN's twenty-year vision.

Ecosystems and climate: fire and aridity

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149   An understanding of ecosystem–climate

150   interactions is the foundation of forecasting

151   ecosystem responses to climate change (Fig.

152   2; Beringer *et al.*, 2015), assuming that such

153   predictability is accurate enough to be
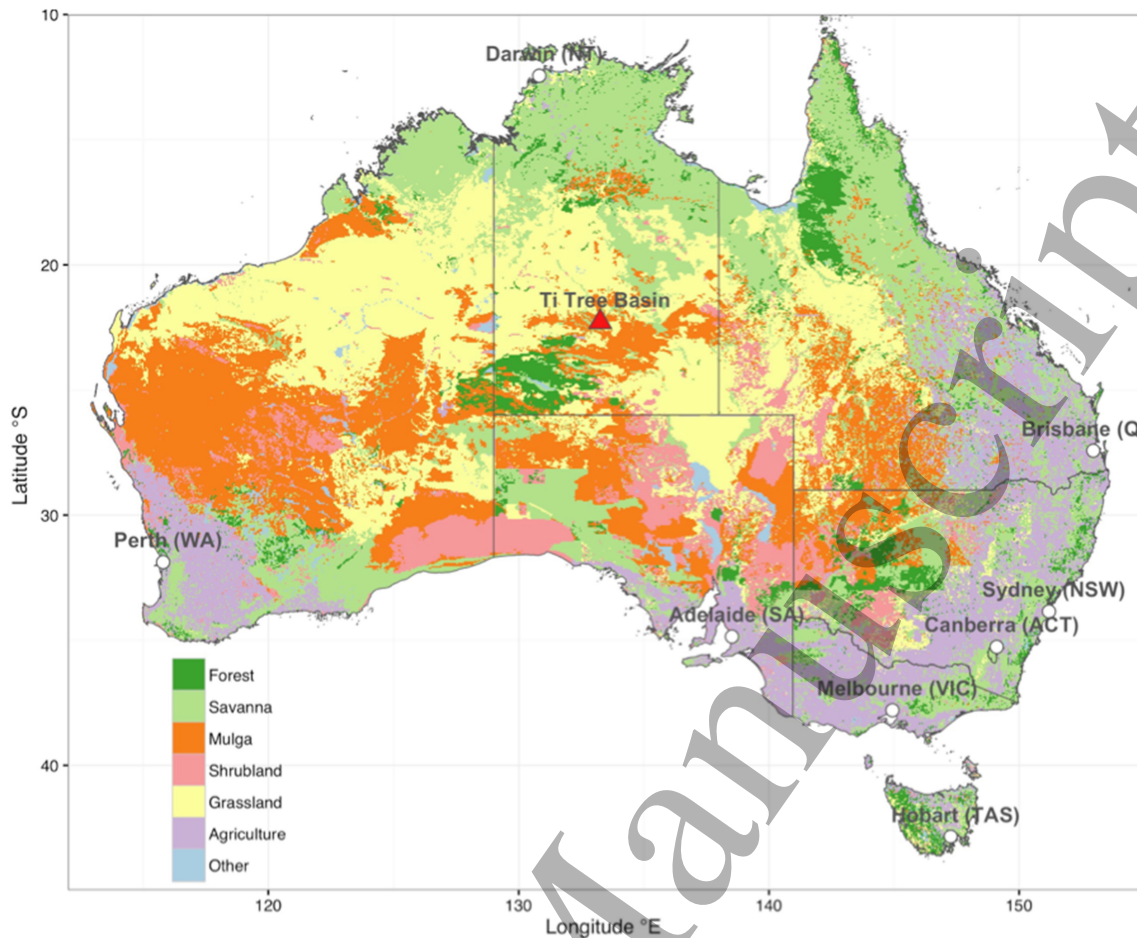
154   feasible (Haughton *et al.*, 2018a).

155   Environmental RI in the form of ecological

156   observatories provides a platform for

157   improved understanding of how ecosystems

Figure 2. The important relationships between ecosystem and climate for savannas exposed to fire. From Beringer *et al.* (2015), CC-BY-NC, used by permission.

158   respond to climate across a diversity of vegetation types. In Australia, 32 major vegetation

159   types have been identified in a national vegetation information system (NVIS;

160   https://www.environment.gov.au/land/native-vegetation/national-vegetation-information-

161   system), although they can be simplified by combining similar types (e.g., arid and semi-arid

162   *Acacia* forests, woodlands, shrublands and savannas are three major vegetation types which

163   are all defined by a dominant canopy of Mulga *Acacia*). By example in a review of key

164   findings from research using TERN RI at the Alice Mulga SuperSite of the Ti Tree basin,

165   Eamus *et al.* (2016) grouped NVIS vegetation types into forest, savanna, Mulga, shrubland,

166   grassland and agriculture (Fig. 3). Across these landscapes, fire and aridity are key forces

167   shaping ecological relationships with climate.

168   Bushfire is a primary attribute of the tropical wet-seasonal savannas and semi-arid

169   grasslands of western and northern Australia, where annual fire frequencies are common

170   across the northern tropical savanna (cf. Figs. 2 and 4). The concentration of TERN

171   infrastructure in northern Australia at intermediate longitudes is organised around the North

172   Australian Tropical Transect (NATT; Fig. 1) to support savanna research across a very large
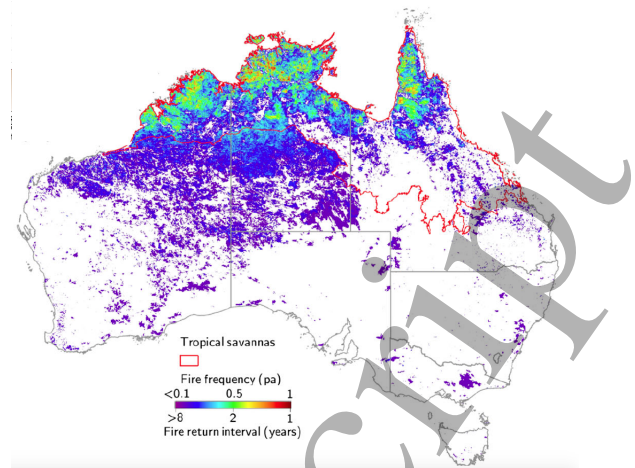
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Figure 3. Distribution of major vegetation types in Australia. Map was generated based on Australia's National Vegetation Information System—Major Vegetation Groups (NVIS-MVGs). Groups were obtained by reclassifying the original 26 NVIS-MVGs. From Eamus *et al*. (2016), CC-BY.

173   precipitation gradient (320 to >1200 mm annual precipitation; Hutley *et al.*, 2011; Cleverly *et*

174   *al.*, 2013; Ma *et al.*, 2013). Heavy rainfall during the wet season at northernmost locations

175   along the NATT is associated with a large accumulation of biomass (Hutley *et al.*, 2011), and

176   this grassy biomass cures over the subsequent dry season that lacks rainfall, leading to the

177   very high frequency of fire re-occurrence at the northern end of the NATT (*ca*. 1–2 years;

178   Fig. 4). Fire is responsible for the majority of productivity losses in the northern savanna

179   (63%), whereas large weather events such as cyclones contribute very little to the long-term

180   net biome carbon budget (Hutley *et al.*, 2013). Burning is furthermore largely responsible for

181   greenhouse gas emissions from savannas and consequential greenhouse gas forcing of

182   climate (Bristow *et al.*, 2016), amongst a cascade of indirect feedbacks between climate and

183   ecosystems which are mediated through local atmospheric dynamics (Fig. 2; Beringer *et al.*,

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184   2015). The outcome of this work is that it has

185   contributed to a better understanding of

186   tropical savanna functioning globally, where

187   similarities of savanna structure have been

188   found to conceal large differences across

189   continents amongst vegetation, climate and

190   fire dynamics (Lehmann *et al.*, 2014).

191   Without studies of savanna function such as

192   these which were enabled by TERN RI (and

Figure 4. Frequency of extensive fires (>4 km^2) across Australia (1997–2013) derived from the AVHRR burnt area product. From Beringer *et al.* (2015), CC-BY-NC, used by permission.

193   similar RI on other continents), a large gap would exist in the understanding of the

194   differences in savanna function globally.

195   Outside of the tropics, bushfire tends to follow two patterns. In drylands, fires occur as a

196   result of fuel accumulation directly following the conclusion of very wet periods, whereas in

197   sclerophyllous eucalypt forests, wildfires occur following drought, once fuel has cured

198   sufficiently (Griffin *et al.*, 1983; Bradstock, 2010). At TERN's Calperum Mallee SuperSite

199   (FLUXNET code AU-Cpr) in a Mediterranean climate, bushfire can have little or no effect

200   on soil respiration, but net ecosystem productivity (NEP) and thus gross primary production

201   (GPP) can be reduced following fire (Sun *et al.*, 2015; Sun *et al.*, 2016; Sun *et al.*, 2017b).

202   Bushfire plays an important role in shaping Australian landscapes, but its observation by

203   environmental RI is limited in time and space, and each event provides a few more hints

204   toward a better understanding of ecosystem responses to fire.

205   Seventy per cent of Australia is arid or semi-arid (Eamus *et al.*, 2006), where aridity is

206   likely to dominate over warming and low levels of soil phosphorus in determining adaptation

207   to future climate (Steane *et al.*, 2017). For example, fauna such as ants, termites and lizards

208   in the Australian tropical savanna are arid-adapted and are thus likely to be resistant to future

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209   increases in aridity (Andersen *et al.*, 2015). By contrast, species in the arid–Mediterranean

210   ecotone are fully adapted to neither climate and are thus sensitive to variations in climate,

211   both spatial and those projected for the future (Guerin *et al.*, 2016). With aridity increasing

212   globally, international integration of environmental RI organisations create further

213   opportunities for discovering diversity responses to aridity.

214   Climate factors associated with aridity include temperature, vapour pressure deficit, solar

215   radiation, precipitation and water availability. Aridity is moreover associated with patterns of

216   water-use efficiency, light-use efficiency, species richness, productivity and adaptability of

217   leaf traits to native growth conditions (Shi *et al.*, 2014; Gibson *et al.*, 2017; Rumman *et al.*,

218   2018; Bloomfield *et al.*, 2019). Grasslands are an important and widespread community

219   across the drylands of Australia (Fig. 3), where climate dynamics are closely related to leaf

220   tissue nutrients (Anderson *et al.*, 2018). To meet the global challenge of understanding

221   nutrient dynamics in grasslands, TERN is partnered with the Nutrient Network (NutNet) at

222   the Great Western Woodlands SuperSite of southwestern Australia (FLUXNET code AU-

223   GWW, NutNet site Mt. Caroline) (Seabloom *et al.*, 2015; Firn *et al.*, 2019). Established to

224   test competing hypotheses for causal mechanisms of relationships between productivity and

225   species richness, initial results from NutNet indicate that climate factors related to aridity

226   such as temperature and the amount and timing of precipitation are positively related to both

227   richness and productivity (Grace *et al.*, 2016).

Ecosystems and climate: climate variability and extreme events

229   Australia's climate is highly variable, with the cultural and economic significance of this

230   highly variable climate illustrated in the well-known common parlance as "a land … of

231   droughts and flooding rains" (Dorothea Mackellar,

232   https://www.dorotheamackellar.com.au/archive/mycountry.htm). A full range of vegetation

233   and climate conditions are currently under-sampled by environmental RI globally (Jones *et*

234   *al.*, 2017), thus the high temperature anomalies experienced by Australian ecosystems

235   provides the world with an important end-member for developing an understanding of

236   ecosystem responses to climate extremes (e.g., heatwaves; De Kauwe *et al.*, 2019).

237   Australia has recently experienced an increase in the frequency and severity of climate

238   extremes (e.g., drought, flooding, heatwave; Cleverly *et al.*, 2016a; Ellis and Albrecht, 2017),

239   and fire has mediated biodiversity responses to this rise in climate extremes in a biome-

240   specific manner (Greenville *et al.*, 2018). For example, many of the grasslands and savannas

241   of Australia are pyrophytic or 'fire promoting', generating large conflagrations in response to

242   a highly variable climate, either seasonally or episodically (Nicholas *et al.*, 2011; Beringer *et*

243   *al.*, 2015; Wright, 2018). By contrast, other vegetation associations like the Mulga (*Acacia*

244   spp.) lands (shrublands, woodlands and savannas) which cover one-fifth of the Australian

245   continent as shown in Figure 3 (Bowman *et al.*, 2008) are sensitive to fire, but they also act as

246   a fire retardant (Murphy *et al.*, 2010). Instead of burning, these ecosystems show adaptations

247   to extreme climate fluctuations with large variations in water-use efficiency, allowing them to

248   exert control on drainage and recharge which is unaffected by variability in hydroclimate

249   (Chen *et al.*, 2014; Chen *et al.*, 2016). Across this myriad of different vegetation types and

250   responses to extreme climate variability, adaptation to environmental variability in

251   temperature and water availability in Australia is associated with gene regions (instead of

252   complete genomes) (Christmas *et al.*, 2016a) and has led to synchronisation of landscape

253   productivity and greenness with hydroclimatic extremes (Cleverly *et al.*, 2013; Ma *et al.*,

254   2015; Rammig and Mahecha, 2015).

255   Ultimately, climate and weather are influenced by ocean–atmosphere interactions within

256   ocean-basin modes of variability. For example, El Niño–Southern Oscillation (ENSO) is

257   driven by a seasonal gradient of sea-surface temperature along the equatorial Pacific Ocean

258   (Trenberth, 1997), and fluctuations between the warm phase (El Niño) and the cold phase (La

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259   Niña) generally bring contrasting conditions to Northern and Southern Hemispheres. El Niño

260   is associated with maritime wet conditions to the Northern Hemisphere and dry conditions

261   across the Southern Hemisphere, whereas La Niña is associated with reversed impacts on

262   precipitation and consequently ecosystems (Holmgren *et al.*, 2001). Data from TERN RI

263   have been used to demonstrate that Australia shows continental phenological responses to

264   ENSO-driven climate variability (Broich *et al.*, 2015) and that litterfall in the tropical

265   rainforest of northeastern Australia is mainly driven by fluctuations in maximum

266   temperature, which are related to ENSO (Edwards *et al.*, 2018).

267   Although ENSO provides the dominant climate signal for global weather patterns, it is

268   becoming apparent that ENSO alone cannot fully explain differences in regional climate

269   variability. Strong coupling amongst the tropical Pacific, Atlantic and Indian Oceans can

270   impact the state of the climate, although limitations still exist in our ability to project future

271   climate without including these teleconnections in climate models (Cai *et al.*, 2019). In

272   Australia, extreme climate variability (floods, droughts, heatwaves) and resultant effects on

273   water resources have been explained by interactions of the three nearest climate modes:

274   ENSO, the Indian Ocean dipole (IOD) and the Southern annular mode (SAM) in the Southern

275   Ocean (Ummenhofer *et al.*, 2009; Ummenhofer *et al.*, 2011; Perkins *et al.*, 2015; Cleverly *et*

276   *al.*, 2016a; Xie *et al.*, 2016; Rogers and Beringer, 2017).

277   The relative strength of a particular climate mode depends upon a given continent's

278   location and the relative importance of direct (i.e., baroclinic) or indirect effects (i.e., Rossby-

279   wave propagation) of the surrounding climate modes (Cai *et al.*, 2011). For example in the

280   northern savanna of Australia, TERN RI was used to show that interannual variability in

281   productivity is associated with climate variability in SOI (Moore *et al.*, 2018). In southern

282   and central Australia, ENSO, IOD and SAM each contribute to variability in rainfall (He and

283   Guan, 2013; He *et al.*, 2014; Cleverly *et al.*, 2016a), and as a result of TERN RI, Australian

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284   ecosystems have been shown to be very resilient to these high levels of rainfall variability

285   (Cleverly *et al.*, 2016b; Cleverly *et al.*, 2016c; Ma *et al.*, 2016).

Wet extremes: flooding rain

287   The two wettest events on record in Australia occurred in 1973–1976 and 2010–2012,

288   both bringing widespread flooding nationally (Meyer *et al.*, 2015; Cleverly *et al.*, 2016a;

289   Cleverly *et al.*, 2016b; Whelan and Frederiksen, 2017). In this letter, we focus on the more

290   recent event, which overlapped with the establishment of TERN. Augmentation of

291   precipitation in the Southern Hemisphere during this very strong La Niña was so large that

292   ocean levels reversed their long-term trend and dropped by 5 mm (Boening *et al.*, 2012;

293   Fasullo *et al.*, 2013). As a result, much of Australia's dryland flushed with greenness in

294   satellite retrievals of both the normalised difference vegetation index (NDVI) and the

295   enhanced vegetation index (EVI) (Wardle *et al.*, 2013; Cleverly *et al.*, 2016a), leading to

296   several ecological responses. Plagues of rats emerge during wet extremes which are absent

297   during dry times (Greenville *et al.*, 2013). Masting occurred in dryland plants, with

298   reproductive structures increasing in mass 300–7000% during 2010–2012 (Travers and

299   Eldridge, 2013). An ecosystem-wide compositional shift occurred in the Simpson Desert,

300   with rooting patterns and soil texture explaining phenological timing and distribution of each

301   plant form (annual grasses and forbs, perennial grasses, shrubs; Nano and Pavey, 2013). Wet

302   extremes have the potential to transform the ecology of vast portions of Australia.

303   Increased water availability resulted in an asymmetrically large increase in CO_2 uptake

304   by semi-arid and temperate regions of Australia, Africa, South America and India (Fig 5;

305   Haverd *et al.*, 2017), with the majority of this global land C sink anomaly located in Australia

306   (Poulter *et al.*, 2014). Carbon fluxes and phenology measured by TERN's RI in semi-arid

307   and Mediterranean climates of Australia confirmed the continent's role in the 2011 global

308   land C sink anomaly (Cleverly *et al.*, 2013; Eamus *et al.*, 2013b; Ma *et al.*, 2015; Sun *et al.*,

14

309   2018). Photosynthesis and respiration are

310   limited by water availability across much of

311   Australia, with both responding positively to

312   extreme precipitation (Cleverly *et al.*, 2013;

313   Haverd *et al.*, 2016) and thus maintaining

314   relatively small NEP and reduced carbon-

315   use efficiency (i.e., NEP / GPP) during wet

316   extremes. Low carbon-use efficiency during

317   wet conditions and water limitations on soil

318   respiration during subsequent dry periods

Figure 5. Asymmetric response of gross primary production (GPP) to precipitation. GPP of semi-arid environments are asymmetrically responsive to wet conditions, whereas mesic ecosystems are asymmetrically responsive to drought.   From Haverd *et al.* (2017), © 2016 John Wiley & Sons Ltd., used by permission.

319   contribute to minimisation of carbon emissions after the conclusion of the wet extreme, in the

320   absence of abiotic decomposition (Cleverly *et al.*, 2013; Cleverly *et al.*, 2016c).

321   Multiple aspects of the climate contributed equally to increased CO_2 uptake in Australia

322   (Trudinger *et al.*, 2016), showing the 2011 global land C sink anomaly to be an integrated

323   climatological, meteorological and ecosystem event (Cleverly *et al.*, 2016a). However, there

324   were two restrictions on Australia's contribution to the land C sink anomaly. First, the

325   asymmetric response of photosynthetic productivity to precipitation is dependent upon

326   antecedent conditions, either amplifying or dampening their relationship (Sun *et al.*, 2017a).

327   The land C sink anomaly followed the driest and hottest year of the Millennium Drought,

328   thus antecedent water resources were at a minimum (van Dijk *et al.*, 2013). Second, energy-

329   limited ecosystems did not show a similar asymmetric response to extrinsic forcing by

330   precipitation and thus did not respond to climate forcing during the land C sink anomaly in

331   the same way that semi-arid ecosystems did (Fig. 5; Haverd *et al.*, 2017). Thus, the

332   contribution of enhanced productivity in coastal, energy-limited ecosystems was expected to

333   be small, whereas Australia's vast drylands have a high capacity for enhanced productivity

334 during wet extremes (Fig. 5). Even with these limitations, the land C sink provided an

335 ecosystem service which might have helped to slow the rate of climate change (Keenan and

336 Williams, 2018).

337 An inevitable outcome of increased productivity is biomass accumulation, especially

338 across grasslands globally, where biomass accumulation is related to climate variability

339 (Morgan *et al.*, 2016). Reduced diversity can result with the presence of a single species of

340 invasive grass (e.g., buffel grass, *Cenchrus ciliaris*), which burns hotter and more completely

341 than native grasses (Schlesinger *et al.*, 2013). For hummock grasslands which cover one-

342 quarter of the Australian land area (Bowman *et al.*, 2008), the legacy of biomass accumulated

343 during the 2011 land C sink anomaly persisted in the absence of burning for years as a strong

344 carbon source due to photodegradation of the standing leaf litter (Cleverly *et al.*, 2016c). C

345 budgets like those of hummock grasslands are very difficult to predict using land surface

346 models (Haughton *et al.*, 2018a) due to a lack of theoretical foundation for the modelling of

347 abiotic decomposition. This is thus an active area of research for which TERN's

348 environmental RI will play an important role in integrating measurements, monitoring,

349 modelling and remote sensing of carbon and water balances (Eamus *et al.*, 2016).

Dry extremes: drought and heatwave

351 Interannual variability in the global carbon cycle is strongly related to the large

352 variability of the semi-arid land C sink (Ahlström *et al.*, 2015). In a single example, the 2011

353 land C sink in Australia was immediately followed by the return of drought and associated

354 heat, which shut down the Australian land C sink even whilst total water storage on the

355 continent had persisted (Fig. 6; Fasullo *et al.*, 2013; Ma *et al.*, 2016). Thus, photosynthetic

356 productivity of Australia is sensitive to meteorological drought (i.e., months to years of

357 below-normal precipitation) and agricultural drought (i.e., yield reduction due to soil drying),

358 but Australia's hydroclimatic variability can moderate against a more severe hydrological

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359   drought (i.e., decline of water storage below the long-term mean; Fig. 6; Dai, 2011). Even

360   during long-term drought, moderately wetter-than-average years can have a strong positive

361   effect on total water storage and productivity across Australia (Fig. 6). The Millennium

362   Drought of 2001–2009 was the longest meteorological drought on record in Australia, but

363   antecedent hydrological drought began in 1994 (van Dijk *et al.*, 2013). During the

364   Millennium Drought, a worldwide reduction in photosynthetic productivity was attributed to

365   drying in the Southern Hemisphere (Zhao and Running, 2010). Despite a widespread and

366   severe reduction in CO_2 uptake during the Millennium Drought, Australian vegetation has

367   shown resilience to a drought as extreme as even it was (Fig. 6; Campos *et al.*, 2013; Ma *et*

368   *al.*, 2013; Ma *et al.*, 2015).

369   Australia has experienced much dryer, longer droughts during previous glacial maxima

370   (Martin, 2006), and this long history of drought has conferred a level of adaptation in

371   Australia's vegetation. At the mesic end of the aridity gradient, the structure of tropical
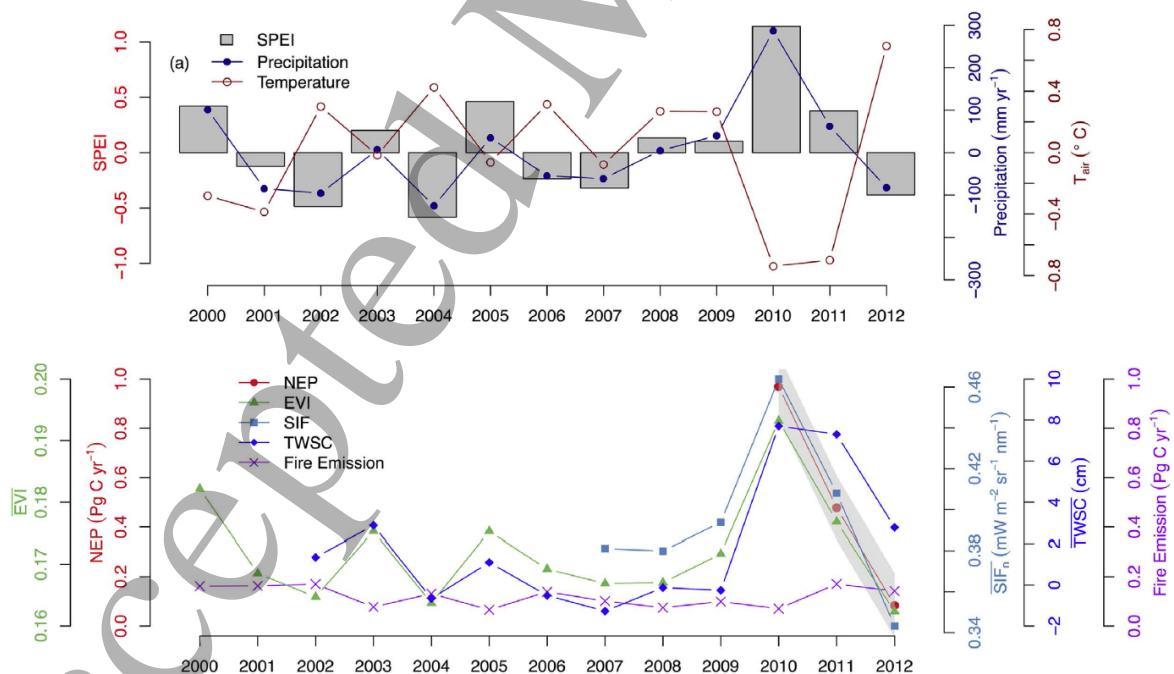
Figure 6. Interannual variation in climate, carbon fluxes and water resources, 2000–2001 through 2012–2013. Shown are a drought index (standardised precipitation–evapotranspiration index, SPEI), precipitation, air temperature (T_{air}), enhanced vegetation index (EVI), net ecosystem productivity (NEP), satellite solar-induced fluorescence (SIF), GRACE total water storage anomalies and fire CO_2 emissions. From Ma *et al.* (2016), CC-BY.

17

372 rainforest trees is adapted to the maximum historical water deficit (Pfeifer *et al.*, 2018). In

373 the more arid-adapted Mallee, a multi-stemmed eucalypt which is also fire adapted, survival

374 of common dry periods is achieved by maintaining conservative (i.e., very small) rates of

375 transpiration (Meyer *et al.*, 2015). Two sequential years of much below-average precipitation

376 in central Australia (mid-2011–2013) resulted in a shift from a strong carbon sink to a carbon

377 source, whilst showing resilience during the subsequent return of average annual

378 precipitation amounts (Cleverly *et al.*, 2016b; Cleverly *et al.*, 2016c). Australian ecosystems

379 show a diversity of hydraulic traits, the presence of which confers resilience to water stress

380 (Nolan *et al.*, 2017; Anderegg *et al.*, 2018).

381   Heatwaves have been increasing in frequency worldwide over the last 20–50 years, and

382 they have been either combined with drought or have occurred under wet conditions,

383 although heatwaves are more commonly associated with drought (Ding and Qian, 2011;

384 Bastos *et al.*, 2014; Teskey *et al.*, 2015; Kang and Eltahir, 2018). Three characteristics of

385 heatwaves, their frequency, intensity and duration, are projected to continue increasing

386 through the end of the 21st century (Perkins-Kirkpatrick *et al.*, 2016). For example, the

387 drought and heatwave which struck Europe in 2003 was so severe and so far outside of the

388 historical record that the return interval estimates are in the range of thousands to millions of

389 years (Schar *et al.*, 2004), but another similar heatwave is expected to occur within the next

390 30 years (Russo *et al.*, 2015). The combination of heatwave and drought, also known as

391 global change-type drought, can have consequences on ecosystems as severe as tree mortality

392 and forest dieback (Breshears *et al.*, 2009; Eamus *et al.*, 2013a), and the likelihood of

393 mortality is expected to increase as the frequency, intensity and duration of heatwaves

394 increases.

395   Soil-moisture–temperature and soil-moisture–precipitation feedbacks are important for

396 development and maintenance of Australian heatwaves, albeit not as important as these

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397   mechanisms are for European heatwaves (Perkins *et al.*, 2015). Drier-than-average

398   conditions in Australia's interior push hot, dry winds into southern Australia from The North

399   (Griebel *et al.*, 2016). One Australian example was the 2012/2013 'Angry Summer'

400   heatwave, which developed as drought across the interior of the continent, and an associated

401   high-pressure ridge pushed high temperatures into forests and woodlands of southern

402   Australia (Cleverly *et al.*, 2016c; van Gorsel *et al.*, 2016).

403   Ecosystem functional responses to both phases of the 'Angry Summer' heatwave (dry

404   followed by wet) were evaluated using TERN's flux tower infrastructure at seven TERN

405   ecosystem processes sites across southern Australia (van Gorsel *et al.*, 2016). NEP and GPP

406   declined sharply during the heatwave in Mediterranean woodlands and dry sclerophyll

407   forests, although reductions were smaller during the wet phase than during the preceding dry

408   phase (Fig. 7). By contrast, the wet sclerophyll forest at the Tumbarumba SuperSite

409   maintained NEP and GPP at constant levels as before the heatwave, with evaporative cooling

410   ameliorating the heatwave and weakening land–atmosphere feedbacks (Fig. 7; van Gorsel *et*

411   *al.*, 2016). However, soil moisture reserves were nearly depleted in the wet sclerophyll forest

412   during the relatively short 'Angry Summer' heatwave, showing afternoon reductions of NEP

413   and GPP during the dry portion of the heatwave, which is consistent with a photosynthetic

414   and stomatal down-regulation due to stress (cf. Fig. 7, Cowan and Farquhar, 1977). Thus,

415   this heatwave provided a second example of the associated effects of drought and heatwave

416   on ecosystem productivity of Australian ecosystems (cf. Figs. 6 and 7) and further

417   demonstrates that increases in the intensity, frequency or duration of heatwaves in future

418   might have seriously detrimental consequences for even Australia's wettest forests (van

419   Gorsel *et al.*, 2016).
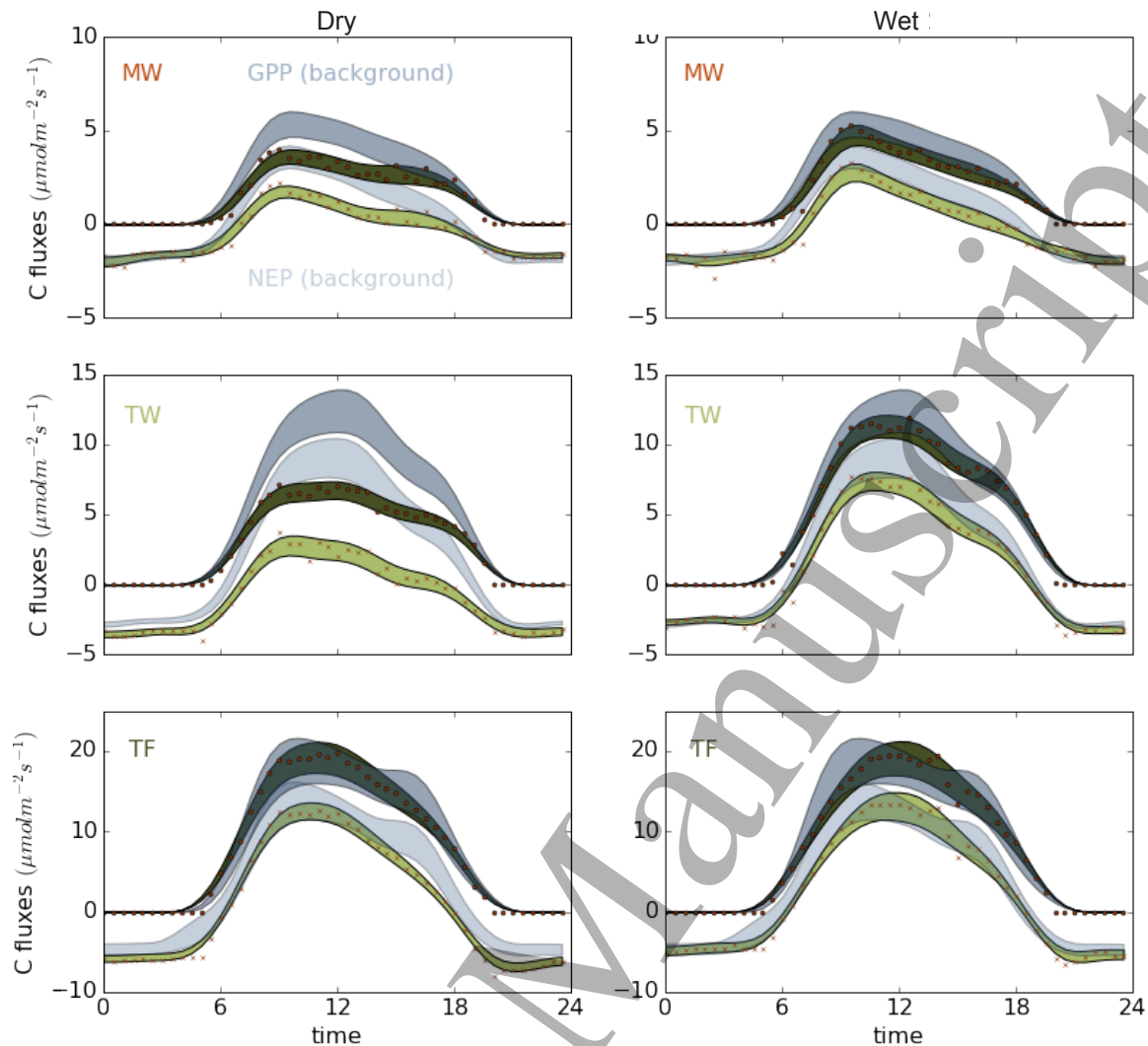
Figure 7. Ecosystem productivity responses to the 'Angry Summer' heatwave in Australia, summer 2012–2013. The initial dry heatwave was broken by a brief wet spell and subsequent wet heatwave. Pre-heatwave C fluxes are shown as the grey background curves. GPP and NEP are shown during pre-heatwave (i.e., background; dark grey and light grey, respectively) and during heatwave (dark green and light green, respectively) for Mediterranean woodlands (MW), dry sclerophyll woodland (temperate woodland, TW) and wet sclerophyll forest (temperate forest, TF). MW sites are the driest (orange), TF sites are the wettest (dark green), and TW are intermediate (light green). From van Gorsel *et al.* (2016), CC-BY.

420
421 **Ecosystems and climate: climate change**

422   Ecosystems can be vulnerable to climate change due to restricted gene flow, habitat loss

423 or restricted range (McCallum *et al.*, 2014). However, cool and mesic locations in the

424 landscape can often provide refugia where higher resilience is encountered than would be

425 otherwise predicted (Guerin *et al.*, 2013; Tapper *et al.*, 2014; Christmas *et al.*, 2017).

426 Refugia on mountains and islands can buffer genetic diversity against a fluctuating climate

427 (Christmas *et al.*, 2017), although climate change can remain a threat for isolated ecosystems

428   such as for island cloud forests where decreasing precipitation and cloud cover have been

429   observed (Auld and Leishman, 2015). Furthermore, refugia can show a tipping point,

430   described as a point in a spatial climate gradient at which ecosystem composition turns over

431   rapidly (Fig. 8; Guerin *et al.*, 2013; Caddy-Retalic *et al.*, 2017). Tipping points occur at

432   locations along an environmental climate gradient where both the species composition of

433   both generalists and specialists changes (Fig. 8). Such a transition zone would exist at the

434   boundary of a climate refugium, where a turnover of multiple species occurs over a short

435   distance (Fig. 8). The presence of a tipping point carries a further risk from climate change

436   as the locations of tipping points contract toward the centre of a species' range. Long-term

437   ecological RI from various countries worldwide, including Australia, has been joined into the

438   International Long Term Ecological Network (ILTER), which addresses the grand challenge

439   of climate change and the resultant loss of biodiversity which is likely to occur (Mirtl *et al.*,

440   2018).
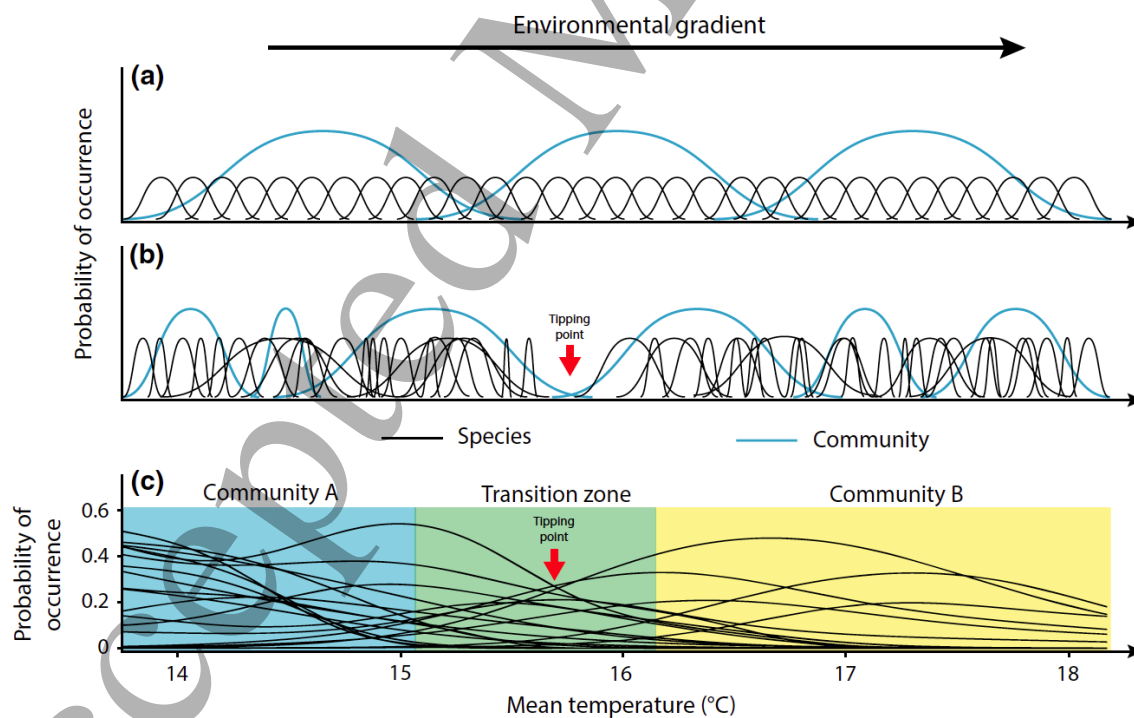
Figure 8. Conceptual diagram of a tipping point along a climate gradient. Tipping points occur where a clear transition occurs for both generalist and specialist species distributions. Panel (a) shows no tipping point and even transitions of community composition along the gradient. Natural ecosystems show a mix of generalists, specialists and intermediate species, with a tipping point (b) or with a tipping point and ecotonal transition zone.   From Caddy-Retalic *et al.* (2017), CC-BY.

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442   Thus far, we have discussed how adaptation, such as adaptation to aridity, can play an

443   important role in protecting biodiversity from climate extremes, but considerations of

444   adaptation and adaptability are also important for biodiversity conservation in a changing

445   climate. Care must be taken, however, to avoid deprioritising refugia which are low in

446   diversity and thereby less adapted to areas outside of their refugium (Costion *et al.*, 2015).

447   Otherwise, several conservation approaches are available for promoting diversity and

448   adaptability to climate change, including

449   climate-adjusted provenancing (Fig. 9),

450   assisted migration, biodiversity corridors and

451   *ex situ* strategies (Prober *et al.*, 2015;

452   Christmas *et al.*, 2016b). In climate-adjusted

453   provenancing, natural genetic variability is

454   exploited to enhance climate resilience of

455   restoration activities over time by predicting

456   future changes in climate over incremental

457   time steps (Fig. 9). This gradual approach

458   over time allows for the detection of

459   uncertainties (e.g., mismatch between

460   predicted and actual climate change

461   trajectories) before it is too late to correct for

462   them (Fig. 9). TERN's plot-based

463   monitoring infrastructure, especially those

464   arrayed in transects along climate gradients,

465   provide a powerful tool for evaluating

466   community responses to climate change and
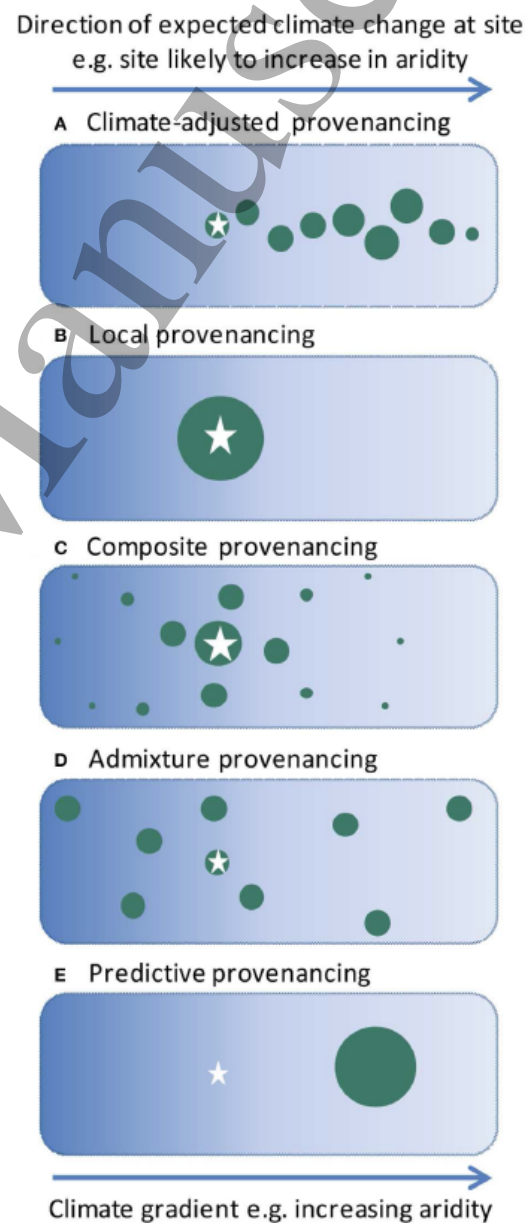
Figure 9. Diagram of provenancing strategies for revegetation in a changing climate.   From Prober *et al.* (2015), CC-BY.

22

467   for promoting resilience in biodiversity (Caddy-Retalic *et al.*, 2017).

468   There are several aspects of projected climate change in relation to ecosystem carbon

469   cycles, such as changes in precipitation, vapour pressure deficit, temperature and elevated

470   [CO_2]. Changes in precipitation seasonality are projected to reduce carbon stocks in the

471   northern Australian savannas and rainforests, even with little change to annual total

472   precipitation (Cook *et al.*, 2015). Increasing vapour pressure deficit during one key season as

473   a result of decreasing seasonal precipitation and increasing temperature is expected to carry

474   detrimental effects upon the carbon cycle of Australian alpine grasslands and tropical

475   rainforests worldwide (Fu *et al.*, 2018; Marchin *et al.*, 2018). Photosynthetic production in

476   tropical rainforests is currently restricted by high vapour pressure deficit, and they are

477   unlikely to tolerate a much drier atmosphere (Fu *et al.*, 2018). In alpine grasslands of

478   Australia, a tipping point has been identified wherein vapour pressure deficits which exceed

479   this threshold can prevent the typical recovery of vegetational greenness at the end of the

480   growing season (Marchin *et al.*, 2018). Increasingly elevated vapour pressure deficit is a

481   serious risk for tree mortality and ecosystem function worldwide (Allen *et al.*, 2010;

482   Breshears *et al.*, 2013; Eamus *et al.*, 2013a).

483   Warming is predicted to have strongly negative effects on Australia's temperate eucalypt

484   forests, nearly 90% of which exist in temperature regimes above their thermal optimum for

485   growth (11°C; Bowman *et al.*, 2014). In the absence of water or substrate limitations,

486   respiration will increase along with rising temperatures, leading to global observations of

487   increasing heterotrophic respiration and climate-driven loss of soil carbon (Bond-Lamberty *et*

488   *al.*, 2018). Acting to counter the effects of increasing temperature, elevated [CO_2] can

489   contribute to maintenance of photosynthesis at reduced stomatal conductance, thereby

490   improving water-use efficiency whilst reducing pressure on limited water resources. CO_2

491   fertilisation is projected to be the main driver of savanna responses to climate, leading to

23

492   increased carbon sequestration in vegetation, although the magnitude of the fertilisation

493   effect will depend strongly upon changes in fire return interval and seasonality (Scheiter *et*

494   *al.*, 2015). Increasing aridity and elevated [CO_2] are likely to affect vegetation dynamics of

495   tropical savannas, which will alter fire regimes and provide further carbon feedbacks to

496   climate (Fig. 2; Beringer *et al.*, 2015).

Final remarks

498   There is an urgent need for environmental information from RI in remote Australian

499   landscapes, which would provide important outcomes and impact related to environmental

500   reporting and fostering research in the framework of global challenges (van Dijk *et al.*, 2014).

501   The risks of climate change as well as opportunities for conservation are emerging from this

502   work, although there is still much to discover. Environmental RIs create the opportunity for

503   identifying and evaluating the key drivers of ecosystem change by allowing researchers to

504   observe state-changing events such as heatwaves, floods or droughts in locations which might

505   be otherwise inaccessible. These are the first steps toward the development of an

506   environmental forecasting system which can answer the global challenge of predicting

507   ecosystem responses to climate change.

Data availability statement

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

515   this study.

24

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Figure captions

1081　**Figure captions**

1082　　**Figure 1.** Map of TERN infrastructure including flux towers in New Zealand as part of

1083　TERN OzFlux. © 2019 TERN at the University of Queensland, used by permission.

1084　　**Figure 2.** The important relationships between ecosystem and climate for savannas

1085　exposed to fire. From Beringer *et al.* (2015), CC-BY-NC, used by permission.

1086　　**Figure 3.** Distribution of major vegetation types in Australia. Map was generated based

1087　on Australia's National Vegetation Information System—Major Vegetation Groups (NVIS-

1088　MVGs). Groups were obtained by reclassifying the original 26 NVIS-MVGs. From Eamus

1089　*et al.* (2016), CC-BY.

1090　　**Figure 4.** Frequency of extensive fires (>4 km^2) across Australia (1997–2013) derived

1091　from the AVHRR burnt area product. From Beringer *et al.* (2015), CC-BY-NC, used by

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1093　　**Figure 5.** Asymmetric response of gross primary production (GPP) to precipitation.

1094　GPP of semi-arid environments are asymmetrically responsive to wet conditions, whereas

1095　mesic ecosystems are asymmetrically responsive to drought. From Haverd *et al.* (2017), ©

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1097　　**Figure 6.** Interannual variation in climate, carbon fluxes and water resources, 2000–

1098　2001 through 2012–2013. Shown are a drought index (standardised precipitation–

1099　evapotranspiration index, SPEI), precipitation, air temperature (T_{air}), enhanced vegetation

1100　index (EVI), net ecosystem productivity (NEP), satellite solar-induced fluorescence (SIF),

1101　GRACE total water storage anomalies and fire CO_2 emissions. From Ma *et al.* (2016), CC-

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1103　　**Figure 7.** Ecosystem productivity responses to the 'Angry Summer' heatwave in

1104　Australia, summer 2012–2013. The initial dry heatwave was broken by a brief wet spell and

1105　subsequent wet heatwave. Pre-heatwave C fluxes are shown as the grey background curves.

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1106   GPP and NEP are shown during pre-heatwave (i.e., background; dark grey and light grey,

1107   respectively) and during heatwave (dark green and light green, respectively) for

1108   Mediterranean woodlands (MW), dry sclerophyll woodland (temperate woodland, TW) and

1109   wet sclerophyll forest (temperate forest, TF). MW sites are the driest (orange), TF sites are

1110   the wettest (dark green), and TW are intermediate (light green). From van Gorsel *et al.*

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1112   **Figure 8.** Conceptual diagram of a tipping point along a climate gradient. Tipping

1113   points occur where a clear transition occurs for both generalist and specialist species

1114   distributions. Panel (a) shows no tipping point and even transitions of community

1115   composition along the gradient. Natural ecosystems show a mix of generalists, specialists and

1116   intermediate species, with a tipping point (b) or with a tipping point and ecotonal transition

1117   zone.   From Caddy-Retalic *et al.* (2017), CC-BY.

1118   **Figure 9.** Diagram of provenancing strategies for revegetation in a changing climate.

1119   From Prober *et al.* (2015), CC-BY.

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