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Australian forested wetlands under climate change: collapse or proliferation?

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Abstract. Climatically driven perturbations (e.g. intense drought, fire, sea surface temperature rise) can bring ecosystems that are already stressed by long-term climate change and other anthropogenic impacts to a point of collapse. Recent reviews of the responses of Australian ecosystems to climate change and associated stressors have suggested widespread ecosystem collapse is occurring across multiple biomes. Two commonly cited case studies concern forested wetland ecosystems: mangrove forest dieback in northern Australia (2015–16) and riverine forest dieback in the south-east of the continent (2002–09). We present an alternative interpretation that emphasises the dominant signal of climate change effects, rather than the interdecadal signal of climate variability that drives wetland forest dynamics. For both the south-east Australian riverine forests and mangroves of northern Australia, aerial extent remains greater after dieback than in the early 1990s. We interpret dieback and defoliation in both systems as a dry phase response and provide evidence of a current and near-future climate change trajectory of increased areal extent and cover (i.e. tree colonisation and range infilling). In both case studies, climate change-driven increases in tree cover and extent are occurring at the expense of wetland grasslands and the important ecosystem functions they support.

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Concerns raised over Australian forested wetlands

The effect of a warming climate on patterns of tree recruitment, growth and mortality is a topic of considerable debate (Allen *et al.* 2015; Hartmann *et al.* 2015). Observations of woody vegetation growth at regional and continental scales suggest an overarching pattern of biomass increase in the absence of local deforestation, an outcome of CO₂ fertilisation, increased water use efficiency, a warmer atmosphere and locally enhanced atmospheric water content (Sittaro *et al.* 2017; Song *et al.* 2018; Wang *et al.* 2018). The expansion of woody vegetation into

grasslands has been described from North America (Van Auken 2009), semi-arid and tropical Australia (Fensham *et al.* 2005), Europe (Maestre *et al.* 2009), India (Misra 1983) and China (Peng *et al.* 2013), contributing to an increase in tree canopy cover across the globe (Song *et al.* 2018). However, the combination of elevated temperatures and severe drought appear to be increasing tree mortality in several biomes, including tropical and boreal forests (Sitch *et al.* 2015; Birch *et al.* 2019; Locosselli *et al.* 2020). The increasing coincidence of drought and higher temperatures ('hotter droughts') is likely to increase the

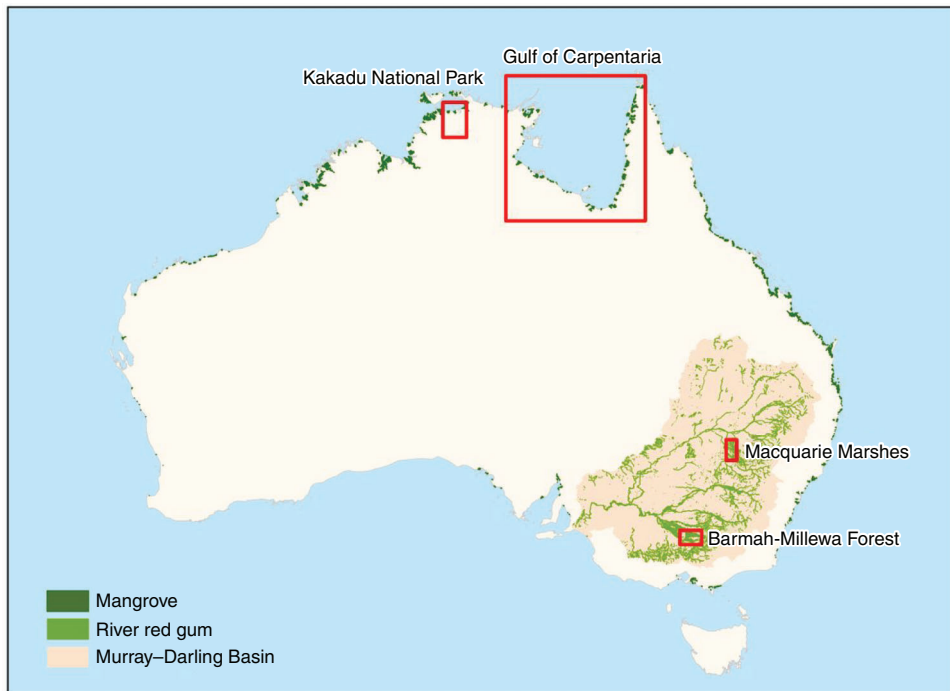


Fig. 1. Spatial distribution of forested wetlands of concern: river red gum forests in the Murray–Darling Basin, and mangrove distribution, showing the locations of Kakadu National Park and the Gulf of Carpentaria.

prevalence and speed of tree mortality under climate change (Allen *et al.* 2015; McDowell *et al.* 2020), increasing the vulnerability of forests already exposed to increased fire risk (Kirchmeier-Young *et al.* 2019) and insect predation (Pureswaran *et al.* 2018).

Short-term extreme climate events, superimposed on the background stress of climate change and other anthropogenic stressors, have been proposed to explain recent widespread changes in Australian ecosystems in recent reviews (Harris *et al.* 2018; Australian Academy of Science 2021; Bergstrom *et al.* 2021). Of these ecosystems of concern, two may be categorised as forested wetlands: mangrove forests of northern Australia and riverine (river red gum) forests of the south-east of the continent (Fig 1). Across the north of Australia, extreme low rainfall corresponding to a negative phase of the El Niño–Southern Oscillation and a positive phase of the Indian Ocean Dipole, coincided with a low sea level anomaly and record high air temperatures contributing to conditions of extreme water stress (Asbridge *et al.* 2016; Bergstrom *et al.* 2021), reducing mangrove cover by ~6% in the Gulf of Carpentaria in 2015 (Duke *et al.* 2017). River red gum forests, the most widespread wetland forests in the south-east of the continent, have been reduced from their pre-European extent due to forestry, land clearing and changes to flood regimes due to irrigation development, with an estimated 60% of the pre-European extent of floodplain forest retained in Victoria and 68% in New South Wales (Mac Nally *et al.* 2011). Widespread declines in the condition of riverine forests occurred throughout the Murray–Darling Basin during the Millennium Drought (Mac Nally *et al.* 2011), a period of prolonged below-average rainfall extending from 1997 to 2010 (van Dijk *et al.* 2013).

Here, we consider trends in mangrove and river red gum forest cover, reviewing the most extensive available mapping (Bowen *et al.* 2017; Lymburner *et al.* 2020; Saintilan *et al.* 2021), applying common mapping protocols to assess changes in spatial distribution and canopy cover through time. Although phases of drought clearly affect canopy condition and mortality rates in both forest types, we provide evidence of an overarching pattern of long-term expansion in forest cover, a likely outcome of global climate drivers. This expansion is associated with a concerning trend of a loss in the extent of wetland grasslands, a vegetation community that makes unique contributions to wetland biodiversity.

Observations of forested wetland resilience and expansion

In common with many *Eucalyptus* species, the river red gum *Eucalyptus camaldulensis* sheds its leaves to reduce transpiration as an adaptation to drought and water stress, but recovers its canopy rapidly by epicormic growth following improvement in soil moisture conditions (Cunningham *et al.* 2007; Doody *et al.* 2015; Souter 2019), as evident during and following the Millennium Drought (Colloff and Baldwin 2010; Wen *et al.* 2012; Wen and Saintilan 2015; Curtis *et al.* 2019). The species can survive decadal-long periods between inundation (Colloff 2014; Doody *et al.* 2015; Shaeri Karimi *et al.* 2021), although with greatly reduced canopy cover. Long-term mapping of some of the most extensive *E. camaldulensis* forests (the Barmah–Millewa Forest and the Macquarie Marshes) using historical aerial photography suggests a substantial increase in extent at the expense of wetland grassland communities over recent decades. For example, in the Barmah–Millewa Forest (35°50'S, 145°00'E), the largest stand of *E. camaldulensis* in Australia,

forest extent has expanded since the 1940s (Bren 1992; Colloff *et al.* 2014; Saintilan *et al.* 2021), primarily into areas previously occupied by flood-dependent Moira grass *Pseudoraphis spinescens*. Under natural recruitment regimes, *E. camaldulensis* stands in the forest were at higher densities and higher canopy cover following the Millennium Drought compared with the historical, pre-logging era in the previous century (McGregor *et al.* 2016). In the Macquarie Marshes (30°43'S, 147°32'E), *E. camaldulensis* forest extent increased between 1991 and 2013 (Bino *et al.* 2015; Bowen *et al.* 2017; Saintilan *et al.* 2021). Although mortality has been reported during and after the Millennium Drought (Catelotti *et al.* 2015), dead trees were clustered primarily in areas that were already identified as stressed (Table 1) during a benchmark survey in 1993 (Bacon 1996).

In the case of the mangroves in northern Australia, the same trend of long-term expansion applies. Progressive landward and seaward extension over the period 1987–2015 was identified using a time-series of Earth observation datasets in Kakadu National Park in the Northern Territory (NT; Asbridge and Lucas 2016) and the Gulf of Carpentaria (Queensland and NT; Asbridge *et al.* 2016). The landward extension was attributed to sea-level fluctuation consistent with trends across the continent (Saintilan *et al.* 2014), facilitating the incursion of salt water (particularly through networks of tidal creeks), leading to greater propagule dispersal, allowing mangroves to establish and, in some cases, rapidly colonise low-lying flood plains (Lucas *et al.* 2018; Asbridge *et al.* 2019).

Landsat-based satellite observations of annual mangrove cover at the continental scale between 1988 and 2017 show an expansion in mangrove extent and a thickening of mangrove canopy cover, particularly since the early 1990s and along low-lying coastal plains (Lymburner *et al.* 2020). Maximum mangrove extent in the Gulf of Carpentaria was attained *c.* 2011 (Fig. 2), with subsequent decline, most obvious in 2015, reversing gains made in the previous two decades (Fig. 2) and affecting mangroves recruited in that period (Asbridge and Lucas 2016; Asbridge *et al.* 2016, 2019; Lymburner *et al.* 2020). The expansion and contraction in mangrove cover in the Gulf of Carpentaria is suggestive of a response to modes of climate and sea level variability (the El Niño–Southern Oscillation and the Indian Ocean Dipole) superimposed on a longer-term trend of increasing extent and canopy cover (Fig 2).

Detailed space- and air-borne observations from the West Alligator River, Kakadu National Park, also show that the extent of mangroves following the 2015 defoliation and dieback was greater than the 1991 reference point due to the longer-term pattern of landward encroachment and on-going seaward expansion in some areas associated with estuary infill and sediment redistributions (Asbridge *et al.* 2019). Phases of contraction and subsequent expansion in extent and canopy cover have occurred previously in relation to El Niño events, associated with reductions in sea levels and an increase in pore water salinity (Lovelock *et al.* 2017).

Consistency with global patterns of change and climate drivers

Tree cover expansion in large wetland complexes in Australia is consistent with trends in wetlands across the globe, covering a wide range of climatic, biogeographical and geomorphological settings. Tree cover expansion has been documented as

Table 1. Branch condition scores in the 1993 survey of Bacon (1996) and in the 2011 survey of Catelotti *et al.* (2015), separating plots identified as stressed and healthy in the Bacon (1996) survey

Branches were scored from 1 (main branch dead) to 5 (no dead branches). Differences in condition are non-significant for healthy plots. Data show the mean \pm s.d. The stressed plots *P*-values are based on paired *t*-tests

	1993	2011	<i>P</i> -value
Stressed plots			
17	2.81 \pm 0.66	3.25 \pm 0.43	0.140
15	1.40 \pm 0.49	0.0 \pm 0.0	0.003
6	2.55 \pm 0.48	0.0 \pm 0.0	<0.001
2	2.95 \pm 0.52	1.48 \pm 1.56	<0.001
4	2.14 \pm 1.03	2.43 \pm 0.82	0.418
8	2.67 \pm 0.59	0.42 \pm 1.11	<0.001
10	2.91 \pm 0.67	0.0 \pm 0.0	<0.001
13	2.68 \pm 0.67	1.9 \pm 1.6	0.093
Healthy plots			
16	3.64 \pm 0.55	2.86 \pm 1.06	0.024
14	3.46 \pm 0.72	2.77 \pm 1.37	0.125
5	3.55 \pm 0.35	2.43 \pm 0.82	0.002
1	3.15 \pm 0.71	2.80 \pm 1.33	0.308
3	3.27 \pm 0.51	2.20 \pm 1.47	0.016
7	3.56 \pm 0.63	2.50 \pm 1.58	0.111
9	3.08 \pm 0.67	0.15 \pm 0.53	<0.001
11	2.67 \pm 0.47	3.00 \pm 0.00	0.348
12	2.50 \pm 0.00	1.33 \pm 0.94	0.164

replacing wetland grasslands in many of the world's most iconic wetlands, including the Pantanal (Barbosa da Silva *et al.* 2016; Arieira *et al.* 2018), the Florida Everglades (Martin *et al.* 2009) and the Okavango Delta, where 27% of open grassland has been replaced by mixed woodland (Hamandawana and Chanda 2010). High-latitude and alpine sedgeland bogs and fens have also been subject to woody encroachment (Elmendorf *et al.* 2012), including on the Qinghai–Tibet plateau (Brandt *et al.* 2013) and in Alaska (Berg *et al.* 2009), Canada (Favreau *et al.* 2019), the US (Stine *et al.* 2011), Europe (Middleton *et al.* 2006) and Tasmania, Australia (Bowman *et al.* 2008).

The drivers of woody encroachment into wetland grasslands, whether inland or coastal, may vary between settings depending on the biophysical characteristics of the landscape and the degree of anthropogenic influences (Saintilan and Rogers 2015). Many changes have been driven primarily by climate, particularly changes in temperature and atmospheric carbon dioxide (CO₂). Increased temperatures have led to changes in the frequency and intensity of wildfires. This has provided opportunities for tree recruitment in dryland savannas (Van Auken 2000; Kgope *et al.* 2010), although a return to historical fire regimes has, in some cases, been insufficient to reverse the trend of woody encroachment (Wigley *et al.* 2010). Warmer temperatures have also allowed altitudinal and latitudinal expansion of tree ranges, and decreased frost frequency has been associated with mangrove proliferation at high latitudes in the US (Cavanaugh *et al.* 2014; Osland *et al.* 2017).

In dryland grasslands at the arid limits of tree growth, elevated atmospheric CO₂ may facilitate woody plant survival by conferring higher water use efficiency (Idso 1992; Polley

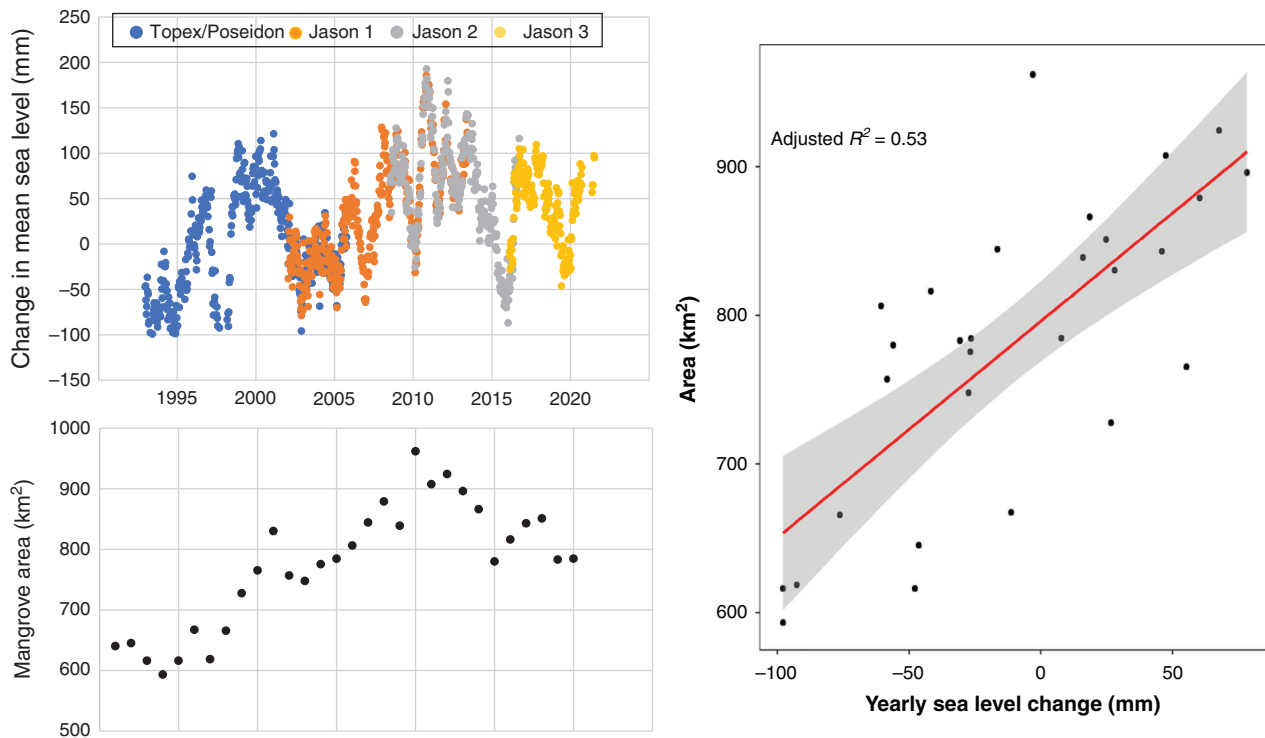


Fig. 2. Mangrove area in the Gulf of Carpentaria and mean regional sea level. Sea level data are derived from satellite altimeters (NOAA/NESDIS/STAR Laboratory for Satellite Altimetry; https://www.star.nesdis.noaa.gov/socd/lisa/SeaLevelRise/LSA_SLR_timeseries_global.php). Mangrove area data and methods are from Lymburner *et al.* (2020). Linear regression analysis of mangrove area indicated by the dotted line ($R^2 = 0.52$; $P < 0.0001$).

et al. 1997). By contrast, many wetland grassland communities gain little benefit from this increase and are being replaced by woody encroachment. These communities include *Sporobolus virginicus* saltmarsh and freshwater grasslands of *P. spinescens* (Moir grass) and *Paspalum distichum* (water couch), which use the C_4 photosynthetic pathway. However, rushes and sedges that use the C_3 pathway, including *Juncus kraussii* in the saltmarsh and *Typha* spp. (cumbungi) in freshwater systems, seem more resistant to colonisation by woody vegetation during and following drought (Saintilan *et al.* 2014, 2021; Sandi *et al.* 2019), although differences in growth habit and location may also confer resilience to larger, thicker rushes and reeds. Atmospheric CO_2 fertilisation may be an important factor contributing to *Eucalyptus* survival on the outer flood plains of Australian semi-arid rivers where water diversions for irrigation have resulted in decreases in the inundation extent and frequency of flood events (Sims *et al.* 2012; Saintilan and Rogers 2015). Elevated CO_2 concentrations may also facilitate mangrove colonisation of ‘physiologically dry’ environments, such as hypersaline upper intertidal saltmarsh, reinforcing the benefit of increased inundation frequency associated with sea level rise (McKee and Rooth 2008).

Implications for wetland grasses and trees

The fate of Australian forested wetlands in a $+3^\circ C$ warmer world may differ from trends observed under current warming (Australian Academy of Science 2021). While we argue that a

continuation of mangrove expansion into northern Australian coastal flood plains is likely during coming decades, there is little evidence to suggest that large mangrove forests can persist *in situ* for long periods under rates of sea level rise projected by the end of the present century under high or even mid-range climate change projections (Saintilan *et al.* 2020; Breda *et al.* 2021). The benefits to tree growth conferred by the CO_2 fertilisation effect may diminish under hotter drought conditions. Such droughts are projected to become more frequent and severe, given the increased prevalence of the dry phase of two key Australian climate drivers in recent decades, namely the Indian Ocean Dipole (Abram *et al.* 2020) and the Southern Annular Mode (Dätwyler *et al.* 2018). An increase in the frequency of short-term mortality events may tip the balance towards river red gum and mangrove forest decline in some settings. These declines may be exacerbated by successive climate events and processes that affect ecosystems in different ways and progressively compromise the ability of ecosystems to recover (Asbridge *et al.* 2018).

On current observations, we expect the immediate effect of climate change will be a continued expansion in the extent of mangrove and river red gum during coming decades. Based on patterns of recent mangrove expansion (Asbridge *et al.* 2016; Lymburner *et al.* 2020) and projections of landward retreat with sea level rise, the trend of mangrove expansion into broad coastal and estuarine flood plains of northern Australia will likely continue (Lovell *et al.* 2015; Schuerch *et al.* 2018; Asbridge *et al.* 2019), furthering the contraction of coastal

floodplain freshwater wetlands in the region (Bowman *et al.* 2010; Saintilan *et al.* 2019).

The capacity for river red gum to survive extended drought by accessing a range of water sources (lateral seepage from rivers, saline groundwater, rainfall and palaeo-channel reservoirs) and reducing water uptake by shedding its canopy (Mensforth *et al.* 1994; Doody *et al.* 2015) makes it unlikely that drought-mediated declines will be widespread or persistent. This is particularly because river red gum is the most broadly distributed *Eucalyptus* species throughout arid Australia and is widespread across a range of climatic and biogeographical settings (Colloff 2014). Reductions in flooding frequency also promote the invasion of reed beds and freshwater grasslands by river red gum (Bren 1992; Colloff 2014; Bowen *et al.* 2017). Although spike-rush (*Eleocharis* spp.) swamps have shown some post-drought recovery (Wassens *et al.* 2017), this has not been observed for the wetland grasslands dominated by *P. spinescens* and *P. distichum*, which may have suffered permanent losses at several locations, often to river red gum (Vivian *et al.* 2015; Wassens *et al.* 2017; Saintilan *et al.* 2021).

The decline of wetland grasslands has important implications for maintaining or enhancing biodiversity, including through conservation and land management and ecosystem restoration. The wetland grasslands of the Murray–Darling Basin are preferred feeding habitat for a diverse range of species, including herbivorous waterbirds (Braithwaite and Frith 1969; Colloff 2014) and mammals (e.g. kangaroos; Iles *et al.* 2010). Temperate coastal saltmarshes that overlap in range with temperate mangrove distribution are used as feeding habitat by migratory shorebirds and endemic grassland birds, many of which are endangered, including the orange-bellied parrot *Neophema chrysogaster*, the yellow chat *Epthianura crocea macgregori* and the slender-billed thornbill *Acanthiza iredalei rosinae* (Spencer *et al.* 2006; Kelleway *et al.* 2017). Three species of threatened microbats, namely *Chalinolobus dwyeri*, *Mormopterus norfolkensis* and *Saccolaimus flaviventris*, were found to feed exclusively in saltmarsh habitats (Gonsalves *et al.* 2012).

Conclusions

The defoliation response of forest wetland trees to drought is easily monitored at broad spatial scales. On the Australian continent, where phases of the El Niño–Southern Oscillation and the Indian Ocean Dipole have driven sharp downturns in canopy extent, these changes have been widely reported. Case studies of forest decline, specifically the mangroves of northern Australia and the river red gum forests of the Murray–Darling Basin, have been posited as exemplars of ecosystem collapse under climate change in recent reviews (Harris *et al.* 2018; Bergstrom *et al.* 2021; and references therein). We have argued that detailed mapping both cases demonstrates an overarching trend of wetland tree proliferation at the expense of wetland grasslands.

Fortunately, from a conservation perspective, the vulnerability of temperate and subtropical coastal saltmarsh to climate change has been recognised, including through their listing as a vulnerable or threatened ecological community under state and commonwealth legislation (Rogers *et al.* 2016). The potential of ‘blue carbon’ benefits also provides a further incentive for restoration under national emissions reduction initiatives

(Kelleway *et al.* 2020). Conservation outcomes for freshwater wetland grasslands have received less attention, despite concerns raised by reserve managers of a trend towards tree monocultures in freshwater floodplain wetlands (Fazey *et al.* 2006). Hence, there is an urgent requirement to consider the future changes in these ecosystems, particularly given further impacts of climate change on water availability and ongoing discussions on environmental water policy, management and allocation (Chen *et al.* 2021; Kirsch *et al.* 2021). This is becoming paramount given that changes in the flooding frequency and depth favour ongoing eucalypt expansion into core grassland habitat.

Data availability

The data used in generating Fig. 1 are available at https://www.star.nesdis.noaa.gov/socd/lisa/SeaLevelRise/LSA_SLR_time-series_global.php and http://dea-public-data.s3-website-ap-southeast-2.amazonaws.com/?prefix=mangrove_cover/v2.0.2/

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Conflicts of interest

Kerrylee Rogers is an Associate Editor for *Marine and Freshwater Research* but did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this Journal. *Marine and Freshwater Research* encourages its editors to publish in the Journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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