



Resilience of trees and the vulnerability of grasslands to climate change in temperate Australian wetlands

Neil Saintilan · Sharon Bowen · Owen Maguire · Sara S. Karimi · Li Wen · Megan Powell · Matthew J. Colloff · S. Sandi · P. Saco · J. Rodriguez

Received: 25 May 2020 / Accepted: 3 December 2020 / Published online: 12 January 2021
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Abstract

Objectives Observations from wetlands across the globe suggest a consistent pattern of woody encroachment into wetland grasslands, altering habitat structure and ecological function. The extent to which hydrological changes have contributed to woody invasion of wetland grasslands is unclear. Our objective was to compare rates of woody encroachment in Australian floodplain wetlands between wet and dry hydrological phases. We test the hypothesis that contraction of non-

woody wetland vegetation (grasses and rushes) would be concentrated in dry phases, co-incident with recruitment of the River Red Gum *Eucalyptus camaldulensis* lower in the floodplain.

Methods We conduct the first detailed mapping of habitat change in two of the largest forested wetlands in inland Australia, comparing wet and dry hydrological phases. Detailed photogrammetry, supported by extensive ground survey, allowed the interpretation of high resolution aerial photography to vegetation community level.

Results We found a consistent pattern of decline in non-woody vegetation, particularly amongst grasses utilising the C₄ photosynthetic pathway. The C₄ grasses *Pseudoraphis spinescens* and *Paspalum distichum* showed steep declines in the Barmah Millewa and Macquarie Marshes respectively, being replaced by River Red Gum *E. camaldulensis*. C₃ sedges proved more resilient in both systems.

Conclusions Our results suggest that a pattern of tree expansion into non-woody wetland vegetation, characteristic of wetlands across the globe, is a major habitat structural change in the Australian floodplain wetlands studied. Projected hydrological impacts of climate change are likely to further restrict wetland grass foraging habitat in these semi-arid floodplain wetlands.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-020-01176-5>.

N. Saintilan (✉) · S. S. Karimi
Department of Earth and Environmental Sciences,
Macquarie University, Sydney, NSW 2109, Australia
e-mail: neil.saintilan@mq.edu.au

S. Bowen · L. Wen · M. Powell
Department of Planning, Industry and Environment, New
South Wales Government, Sydney, NSW 2150, Australia

O. Maguire
GreenCollar, 3 Hickson Rd, Sydney, NSW, Australia

M. J. Colloff
Fenner School of Environment and Society, Australian
National University, Canberra, Australia

S. Sandi · P. Saco · J. Rodriguez
School of Engineering and Centre for Water Security and
Environmental Sustainability, The University of
Newcastle, Callaghan, Australia

Keywords Wetland · Woody encroachment · Canopy condition · Drought · Climate change

Introduction

Tree cover across the globe has increased by 7.1% in the period 1982–2016 (Song et al. 2018) in spite of deforestation leading to local declines in the extent of forests. Global and continental-scale observations of woody vegetation thickening and expansion into grasslands align with those made at a regional scale, including woody encroachment into the savannas and prairies of 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). Less attention has been given to woody encroachment in wetlands, though there is a growing body of evidence to suggest that the recruitment of trees and shrubs into wetland grasslands is widespread and altering the character and function of wetland environments across the globe (Saintilan and Rogers 2015). Woody encroachment has been described replacing sedgeland in high latitude bogs and fens in Alaska (Berg et al. 2009), Canada (Favreau et al. 2019), the conterminous United States (Stine et al. 2011), Europe (Middleton et al. 2006), and Tasmania, Australia (Bowman et al. 2013). The expansion of mangrove into herbaceous coastal marshland has been documented across five continents near mangrove poleward limits (Saintilan et al. 2014). Several of the world's largest seasonally and intermittently flooded wetlands have been sites of significant woody expansion and grassland decline including the Pantanal (Arieira et al. 2018), the Florida Everglades (Quintana-Ascencio et al. 2013), the Okavango (Hamandawana and Chanda 2010), and Kakadu, northern Australia (Bowman et al. 2008). However, an exploration of the causes and consequences of these changes has been lacking.

Several factors might be contributing to improved tree recruitment and survival in wetland grasslands. Indigenous fire regimes in the Pantanal, South America (Junk and da Cunha 2012) and Australia (Bowman 1998) historically excluded trees, and their modification following the introduction of grazing has, in common with many terrestrial grassland settings, reduced the frequency and intensity of fire. However, the restoration of historical fire and grazing regimes in several terrestrial settings has not always halted woody encroachment (Briggs et al. 2005). Hydrological changes may also be an important driver, given the importance of hydroperiod as a control over wetland

vegetation structure. In some settings woody encroachment is associated with wetter conditions (mangrove encroachment in saltmarsh: Rogers et al. 2006; *Vochysia divergens* in the Pantanal grasslands: Nunes da Cunha and Junk 2004) and other places dryer conditions (peatland bogs: Pellerin et al. 2016), while some studies have documented encroachment across the range of hydrological conditions (Bart et al. 2016).

Australia's second largest and most agriculturally important river basin, the Murray-Darling (1.06 million km²), supports several large intermittently flooded wetlands of diverse vegetation assemblage including a mix of woodland vegetation and grassland. The hydrology of Australian inland rivers is strongly influenced by phases in the El Niño-Southern Oscillation (Verdon et al. 2004) and the Indian Ocean Dipole (Ummenhofer et al. 2009). River flow and floodplain inundation patterns are highly variable in space and time (Puckridge et al. 1998) and droughts may last for several years, breaking suddenly. The 1950s and 1970s were characterised by frequent, large floods, and were followed by decades of water resource development and a drying climate trend across the basin. The Millennium Drought (1997–2010) consisted in the longest uninterrupted period of below-average annual rainfall in at least a century (van Dijk et al. 2013). The long continuous period of low inflows and rainfall, co-incident with the suspension of environmental watering arrangements in many catchments led to reductions in floodplain inundation that were historically unprecedented. This drought was broken in 2010 by near record inflows.

Hydrological extremes may shape competitive interactions between trees and grasses on inland ephemeral floodplains. Long duration of inundation can lead to drowning of seedlings and adult trees (Colloff et al. 2014), while extreme inter-flood periods can lead to water stress (Doody et al. 2015) and tree mortality (Catelotti et al. 2015). Frequent spring–summer inundation is important to the growth of wetland grasses and their competitive success against tree seedlings (Colloff et al. 2014). On this basis, woodland-grassland interactions in floodplain wetlands might be conceptualised as occurring along a gradient of disturbance, tree expansion prevailing under low disturbance punctuated by dieback under extremes of wet (low floodplain dieback) and dry (high floodplain dieback) (Fig. 1). The combined impacts of drought, water abstraction and a drying

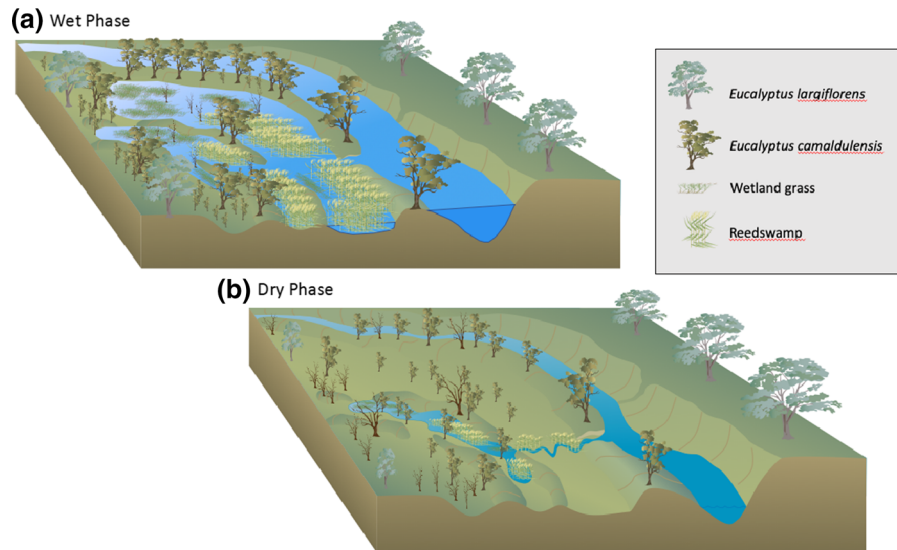


Fig. 1 Conceptual model of floodplain vegetation dynamics in association with wet and dry climate phases in semi-arid Australia. During the wet phase, *E. camaldulensis* is drowned in the inner floodplain and recruits into the outer floodplain, while

non-woody vegetation expands from root stock. During the dry phase, *E. camaldulensis* dies back on the outer floodplain, and is recruited into the inner floodplain, while non-woody vegetation contracts to core refugia

climate trend have raised concerns over the long-term resilience of floodplain forests in rivers subject to water resource development and climate change (Mac Nally et al. 2011; Harris et al. 2018). In this study we apply detailed, visual aerial photographic interpretation in multi-decadal time-series for two of the three largest River Red Gum (*Eucalyptus camaldulensis*) forests in Australia's Murray Darling Basin; the Barmah-Millewa Forest and the Macquarie Marshes (Fig. 2), testing whether tree recruitment and dieback are linked to phases of drought and inundation. Our hypothesis is that the imposition of drought will modulate a long-term trend of woody vegetation expansion by reducing tree extent on the outer floodplain while encouraging recruitment into low-lying wetland areas of reduced herbaceous coverage.

In both the Macquarie Marshes and the Barmah Millewa Forest, our mapping spans the period before, during and following the Millennium Drought, and in the Barmah Millewa Forest prior to the record floods of the 1950s and 1970s. Detailed photogrammetry, coupled with extensive on-ground survey, has allowed identification of trends in the extent of vegetation communities, including forests and woodlands dominated by the River Red Gum *E. camaldulensis* and a range of non-woody wetland vegetation types (sedges, rushes and grasslands). Our aim was to understand the

differing vulnerability of vegetation structural/floristic types to anticipated increases in the frequency and intensity of drought in the Murray-Darling Basin (MDB), a projected outcome of climate change (Chiew et al. 2011). We hypothesised that contraction of non-woody wetland vegetation (grasses and rushes) would be concentrated in dry phases, co-incident with recruitment of *E. camaldulensis* lower in the floodplain, and dieback in the outer floodplain, as previously reported by ground survey (Horner et al. 2009). Conversely, we expected that wet phases would see the recovery of non-woody vegetation, the drowning of *E. camaldulensis* in the lower floodplain and the expansion of the species on the outer floodplain.

Methods

We conducted fine scale mapping of vegetation communities using historic aerial photography in two of the three largest forested wetlands in the MDB: the Barmah-Millewa Forest, and the Macquarie Marshes (Fig. 2). Both forests are listed as internationally important Wetlands under the Ramsar Convention and contain some of the largest remaining wetland grassland in the MDB. In both wetlands, *E. camaldulensis* forms extensive closed forest and open

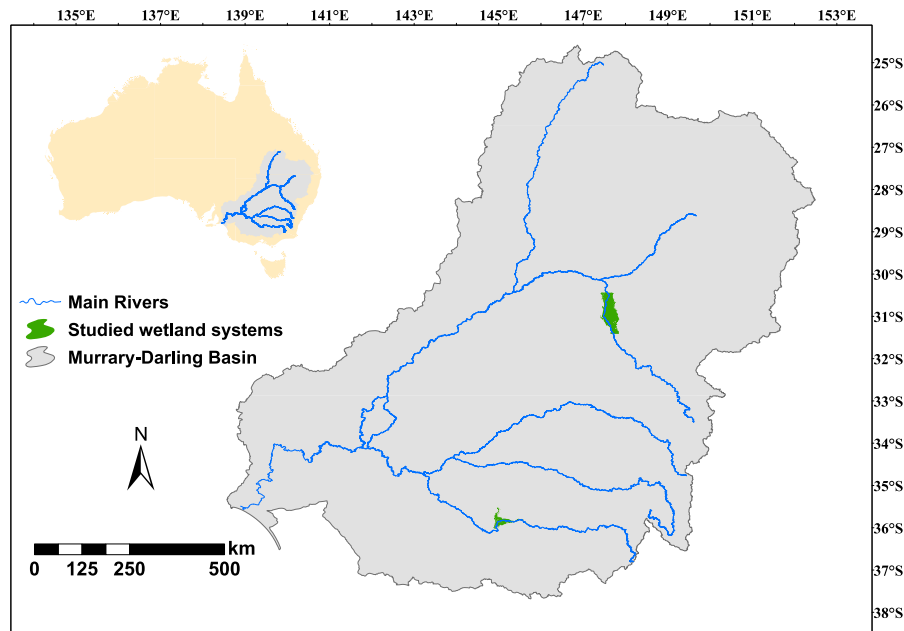


Fig. 2 Location of the Murray Darling Basin, including the large wetland complexes of the Murray, Murrumbidgee and Macquarie rivers

woodland communities. Non-woody wetland vegetation in the Barmah-Millewa Forest has been historically dominated by the Moira Grass *Pseudoraphis spinescens* (Colloff et al. 2014), with the rushes *Juncus ingens* and *Typha domingensis* forming dense patches. In the Macquarie Marshes, wetland grassland is dominated by the Water Couch *Paspalum distichum*, with *Phragmites australis* and *Typha* spp. locally important. Vegetation community boundaries are identifiable from high resolution aerial photography, and in each case our mapping represents the best available long-term (inter-decadal) mapping of *E. camaldulensis* forest and non-woody wetland vegetation community extent, supported by extensive on-ground verification. We explored the interactions between *E. camaldulensis* communities and non-woody (grassland and sedgeland) wetland vegetation, and their contrasting response to drought and re-flooding.

Vegetation mapping

Murray Valley National Park (Moira Precinct) is approximately 9200 ha and is shown in Fig. S3. Four sets of historical imagery were sourced for the Moira Compartment of the Barmah Millewa Forest: 1945

(1:34,000), 1970, 1991 and 2010 (1:50,000). Mapping was not attempted after this date due to the potential confounding effect of *E. camaldulensis* thinning trials conducted by the NSW Government from 2011. Black and white film photography was scanned, given external orientation parameters and subsequently built into stereo models (one for each epoch) so that they could be viewed and interpreted in a digital 3D environment (Stereo Analyst for ArcGIS).

3D visual interpretation of aerial imagery was undertaken in ‘Stereo Analyst for ArcGIS’ using a similar method to Maguire et al. (2012). The attributed linework for Moira (Bowen et al. 2011) was used as a starting point. It was draped over the DEM, thus converting the 2D shapefile to a 3D shapefile able to be displayed and edited in 3D over the 1991 imagery. This new 1991 layer derived from Bowen et al. (2011) was then interpreted over the 1970 imagery to produce the 1970 layer, which was then interpreted over the 1945 imagery to produce the 1945 layer.

Comprehensive mapping of vegetation community extent and condition in the Macquarie Marshes before, during and after the Millennium Drought used high-resolution aerial photography for 1991, 2008 and 2013, and extensive on-ground verification of 200,000 hectares of the lower Macquarie River floodplain,

including the Ramsar-listed Macquarie Marshes Nature Reserve. A map of the vegetation communities of the Macquarie Marshes in 1991 was previously created by manual aerial photo interpretation (API) of 1:50,000 scale black and white aerial photographs and classification of vegetation communities calibrated by ground surveys (Wilson 1992). Vegetation communities in 1991 were determined by dominant species and structural characteristics such as growth form, and density (Johnson et al. 1992). The 1991 map was scanned and ortho-rectified to create a digital shapefile that was then interrogated for vegetation spatial area and type. The original mapping units of Wilson (1992) were renamed to reflect the then current classification of vegetation communities in NSW and then re-assigned to the NSW Plant Community Types described in the NSW Vegetation Information System Classification. The 1991 map was substantially reworked and revised by manual API using digital versions of scanned and ortho-rectified black and white aerial photography first captured in January 1991, viewed on screen to a resolution of 1:1000. Co-incident georeferenced on ground survey data, stored in the NSW Vegetation Information System (VIS) Flora Module (Office of Environment and Heritage 2017), was analysed for vegetation type and condition.

The 2008 and 2013 spatial extent of vegetation communities was delineated by visual API of high-resolution digital colour aerial photographs, taken in July 2008 (30 cm resolution), September 2013 (50 cm resolution), and in six sections of the outer floodplain using 2018 aerial photography (50 cm resolution). Field surveys were completed in May, October and November 2008, and March 2014 to validate the mapping units and their extent and to quantitatively assess their condition (Bowen and Simpson 2008).

Hydrological time series and statistical analysis

Total annual runoff (Q_i) series at the nearest long-term gauging stations were accessed from WaterNSW real-time data website (<https://realtimedata.watarnsw.com.au>), and represented as a percentage deviation (ΔQ) from average annual runoff (Q_{avg}) (Figs. S1, S2), and calculated using Eq. (1):

$$\Delta Q = \left[\frac{Q_i - Q_{avg}}{Q_{avg}} \right] \times 100. \quad (1)$$

Marebone Break gauge station (No. 421088) on the Macquarie River and Yarrawonga gauge station (No. 409025) on the Murray River were selected for this study as they are stations that faithfully represent the conditions in the Macquarie Marshes and the Barmah-Millewa Forest respectively for the time periods of interest. Missing data was synthetically generated using correlations of cumulative runoff volume data recorded in nearby stations. Warren station (No. 421004) and Marebone Weir station (No. 421090) data were used to extrapolate and complete Marebone Break monthly data series which was then used to calculate total annual runoff. Annual runoff series from Yarrawonga station were extrapolated using data from Barham station (No. 409005) located downstream in the Murray River. Data illustrate the protracted Millennium Drought (1997–2010) in both systems; very large inflows into the Macquarie Marshes in 1990, and several years in the 1970s. The Barmah-Millewa Forest received particularly high inflows in the 1950s and 1970s. Regression analysis was performed on vegetation species extent trends through time for the Barmah-Millewa forest (Fig. 3).

Results

The River Murray forests

In the Barmah Millewa Forest (35° 50'S, 145° 00'E), *E. camaldulensis* has expanded since at least 1945 (Colloff et al. 2014), primarily into areas previously occupied by flood-dependent Moira Grass *P. spinescens*. Expansion of *E. camaldulensis* forest may have pre-dated 1945 (the earliest aerial photography available), given descriptions by European explorers, squatters and surveyors in the first half of the 19th Century of grassy wetland plains (Chesterfield 1986; Colloff et al. 2014). Our fine-scale mapping of vegetation communities showed an 11% increase in the extent of *E. camaldulensis* forest in the Moira compartment (the western half) of the Barmah-Millewa Forest and a 78% decline in *P. spinescens* in the period 1945–2010. Much of this expansion in *E. camaldulensis* occurred in decades characterised by extensive flooding, including the 1956 flood (the largest on record). While the Millennium Drought slowed the expansion, no net loss in forest extent was

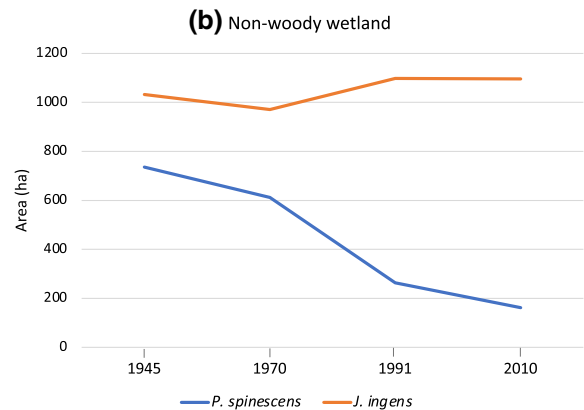
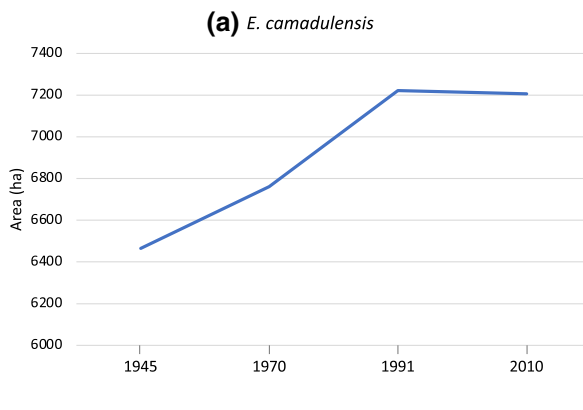


Fig. 3 Inter-decadal trends in the extent of *Eucalyptus camaldulensis* woodland and non-woody vegetation in the western Barmah-Millewa forest. *E. camaldulensis* extent

observed over the drought period (Fig. 3). Giant Rush *J. ingens* was largely resistant to *E. camaldulensis* encroachment (Fig. 3), as was *T. domingensis*. Moira Grass (*P. spinescens*) has declined consistently since 1930, but with no clear association with water availability. Some loss in area of *P. spinescens* has also been attributed to invasion by *J. ingens* (Mayence et al. 2010), a species more suited to long-duration summer flooding in low-lying areas (Vivian et al. 2014).

While the Millennium Drought halted the expansion of *E. camaldulensis* there is no evidence of mortality, in spite of a reduction in canopy cover and ‘vigour’ apparent from remote sensing of Normalised Difference Vegetation Index (NDVI) (Mac Nally et al. 2011). Canopy condition (relative defoliation) measured on-ground to calibrate Landsat7-derived NDVI estimated that 11–16% of Victorian *E. camaldulensis* forest was in the poor condition in 2009.

The Macquarie Marshes

River Red Gum has undergone similar expansion in the largest wetland forest in the northern Murray-Darling Basin: the Macquarie Marshes (30° 43’S; 147° 32’E), which support extensive *E. camaldulensis* forest and woodland in a vegetation mosaic that includes wetland grasses and reedbeds. In spite of the apparent mortality of trees assessed in a tagging study (Catelotti et al. 2015), the extent of *E. camaldulensis* forest was largely unaffected by the drought: there was a 4% increase between 1991 and 2013 (Fig. 4). A

increased over time ($R^2 = 0.91$; $P = 0.04$); while *P. spinescens* extent declined ($R^2 = 0.95$; $P < 0.03$). The trend for *J. ingens* was not significant ($R^2 = 0.42$; $P = 0.35$)

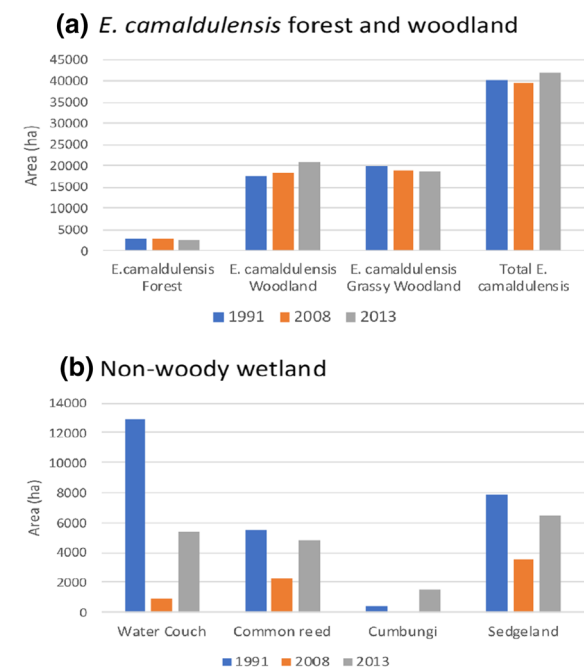


Fig. 4 Floodplain wetland vegetation community extent in the Macquarie Marshes 1991, 2008, 2013. **a** Trends in the extent of *Eucalyptus camaldulensis* communities and **b** non-woody wetland vegetation: water couch *Paspalum distichum*; Common reed *Phragmites australis*; Cumbungi *Typha* spp.) and Sedgeland

decline in *E. camaldulensis* grassy woodland was offset by an increase in *E. camaldulensis* woodland (Fig. 4a), particularly in the eastern portion of the marshes, implying woody thickening and the loss of the grassy understory.

We chose six segments of the outer floodplain for detailed time-series analysis where a previous modelling study (Catelotti et al. 2015) suggested *E. camaldulensis* would have less than 63% chance of surviving the drought (Fig. 5). In all cases the extent of woodland increased between 1991 and 2018. The expansion of River Red Gum since 2010 suggests either the recovery of trees assumed dead or strong recruitment following the breaking of the Millennium Drought in September 2010. This expansion has occurred in spite of reductions in inundation frequency between 1991 and 2008 (Bino et al. 2015), and the longest drought on record.

Non-woody wetland vegetation is adapted to more frequent inundation than floodplain trees and shrubs (Sandi et al. 2019). The spatial extent of dominant Water Couch (*P. distichum*) aquatic grassland, beds of Common Reed (*P. australis*), Cumbungi (*Typha* spp.) and sedges, showed strong decline towards the end of the Millennium Drought in 2008 (Fig. 4). Above-ground biomass was reduced or lost, associated with

reduced inundation (Whitaker et al. 2015), and chenopod shrubs increased in extent from 4 ha in 1991 to 14,847 ha in 2013. Following the breaking of the Millennium Drought in 2010 and two successive years of heavy rainfall and inflows, invasive terrestrial chenopod dominated shrublands all but disappeared (313 ha in 2013), while *P. australis* reedbeds, and sedgeland were restored to within 80–95% of their pre-drought extent. Cumbungi increased to 1533 ha, three times the extent in 1991. An exception to this strong pattern of recovery is the Water Couch *P. distichum*. In 1991 Water Couch aquatic grassland was the most extensive non-woody plant community at the Macquarie Marshes, with over 12,000 ha. By 2013 *P. distichum* had recovered only 40% of its previous extent, with large areas replaced by woody vegetation (*E. camaldulensis* and *Acacia stenophylla*), non woody wetland vegetation (Cumbungi, sedgeland) and terrestrial vegetation (tussock grass).

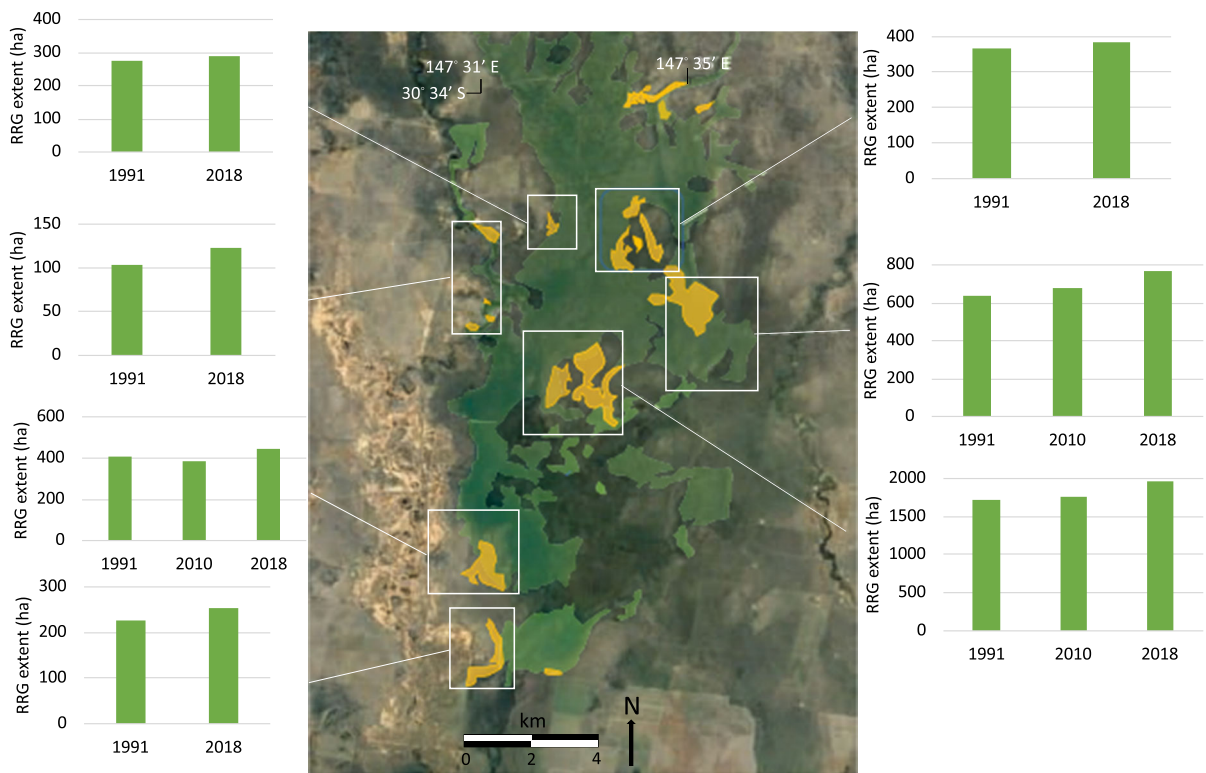


Fig. 5 Distribution of *Eucalyptus camaldulensis* extent (2010) in the northern Macquarie Marshes and trends in extent on the outer floodplain during and following the Millennium drought.

Yellow shaded areas are those modelled by (37) as lower than 0.63 probability of tree persistence following the drought

Discussion

Global trends in wetland grassland decline and possible drivers

Widespread deterioration in canopy condition of River Red Gum *E. camaldulensis* forests during the Millennium Drought was reported from remote sensing and field surveys (Mac Nally et al. 2011; Harris et al. 2018), including apparent mortality of up to 44% in the Macquarie Marshes (Catelotti et al. 2015). However, in spite of several studies applying satellite remote sensing to canopy condition in the MDB, detailed time-series mapping of vegetation communities in MDB wetlands has been lacking, preventing an assessment of change in the extent of woody and non-woody wetland vegetation communities. Contrary to expectation we found an expansion and thickening of the River Red Gum into the grassy wetlands of the MDB through a range of hydrological extremes.

The expansion of tree cover is a trend consistent with observations in other intermittently flooded wetlands. Within the Pantanal, in the Upper Paraguay basin of South America, grasslands are being replaced by invasive trees, most notably the native *V. divergens* (Cambará) (Arieira et al. 2018). When canopy cover exceeds 30%, grassland plants are displaced (Barbosa da Silva et al. 2016), as are anurans (Dorado-Rodrigues et al. 2015). On the North American continent, the Florida Everglades, the once renowned as the “River of Grass” has been extensively colonised by willow and the introduced *Melaleuca quinquenervia* (Martin et al. 2009). Historical aerial photography of the Okavango delta, Africa, documents a 22.5% decrease in open grassland and a corresponding 27% increase in mixed woodland (Hamandawana and Chanda 2010) between 1967 and 2001. On the South Alligator River floodplain in Kakadu National Park in tropical Australia, woody cover increased from 21 to 31% between 1984 and 2004, the mechanism unknown (Bowman et al. 2008).

In the Barmah-Millewa Forest, the invasion of Moira Grass plains by *E. camaldulensis* has been attributed to a reduction in frequency, extent and duration of flood events. Similar observations have been recorded in the nearby Mid-Murrumbidgee wetlands (Wassens et al. 2017) where *E. camaldulensis* recruited heavily in lagoons during the Millennium Drought and *P. spinescens* failed to recover. In both

settings, *E. camaldulensis* is recruiting down the inundation gradient into areas previously too frequently and deeply inundated. While we do not have annual data on extent, high rates of expansion were observed in historically wet decades. It is possible that comparatively wet decades (1950s 1970s Fig. S1) and individual high flood years (1956, 1974) may not have been sufficient to counter alterations to the timing and frequency of flooding introduced by the operation of the Hume Dam (completed in 1936). Further, aquatic, soil and atmospheric CO₂ fertilisation may play a role in accelerating growth rate between floods (Saintilan and Rogers 2015), promoting recruitment down the inundation gradient (Fig. 6).

Perhaps more surprising is the continued expansion of *E. camaldulensis* on the outer floodplain of the Macquarie Marshes during the Millennium Drought. *E. camaldulensis* regulates stomatal conductance during drought, trading off decreased water loss for lower carbon assimilation, at the same time reducing sapwood volume to compensate (Doody et al. 2015). Elevated atmospheric CO₂ allows photosynthesis in C₃ plants to be maintained with lower rates of water loss (Polley et al. 1997); an advantage particularly when C₃ and C₄ plants compete in semi-arid and arid environments (Idso 1992). Further, decreased evapotranspiration resulting from reduced leaf conductance leads to higher soil water content where woody thickening is occurring (Eamus and Palmer 2008; Carol Adair et al. 2011), facilitating deep percolation

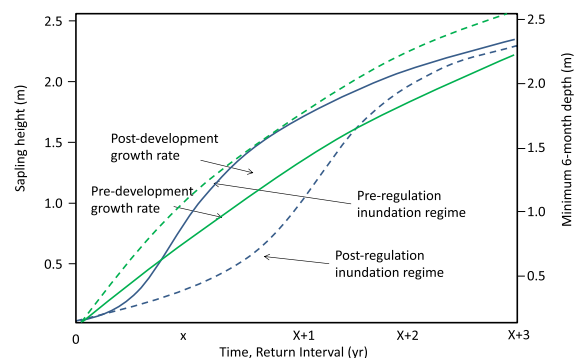


Fig. 6 Conceptual model of the relationship between sapling growth rate and inundation regime on the Moira Grass plains (after Saintilan and Rogers 2015). Inundation regime is represented as the return interval of 6-month continual inundation at depths 0–2.5 m, for natural (solid blue line) and post-development (dashed blue line) conditions. Growth rate is represented as pre-European (solid green line), and current (dotted line), following nutrient and CO₂ fertilisation

and a competitive advantage for deeper rooting plants over grasses. Elevated CO₂ is likely therefore to improve drought resistance of semi-arid floodplain plants that use the C₃ photosynthetic pathway. C₃ reedbeds (*J. ingens* at Barmah-Millewa Forest; *P. australis*, *Typha* spp. and sedgeland at Macquarie Marshes), appear resilient to invasion by *E. camaldulensis*.

The susceptibility of C₄ grasslands to woody encroachment has also been noted in coastal wetlands, where grasslands of *Sporobolus virginicus* (Australia), and *Spartina alterniflora* (United States) have been colonised by mangroves of the genus *Avicennia*. In the Pantanal the C₄ grass associations capim-vermelho (being *Andropogon hypogynus* and *Axonopus lepostachyus*) and capim mimosa (*Axonopus purusii* and *Reimarochloa brasiliensis*) have been particularly prone to invasion by *V. divergens*. In the Macquarie Marshes, the Mid-Murrumbidgee wetlands and Barmah-Millewa Forest, the expansion of woody wetland vegetation has also been primarily at the expense of grasses using the C₄ photosynthetic pathway. We document the substantial decline of Moira Grass *P. spinescens* in the Barmah-Millewa Forest, also noted in the mid Murrumbidgee wetlands (Wassens et al. 2017), as well as Water Couch *P. distichum* at Macquarie Marshes. Little difference has been found in hydrological characteristics of areas lost to *P. distichum* and areas retained (Sandi et al. 2019) whereas the C₃ non-woody vegetation declined preferentially in areas of lower hydroperiod. This would suggest that *P. distichum* is unlikely to be retained under current hydrological and climatic conditions.

Changes in circulation patterns and rainfall are a probable outcome of climate warming over inland Australia of 1–1.2 °C by 2030 and 1.8–3.4 °C by 2070 (Watterson and Whetton 2011). The best estimates of 2030 climate suggest a decrease of 2–5% in rainfall over central areas of the Murray-Darling Basin, translating into a projected decrease of 12% in available surface water (CSIRO 2008). Projected changes in flood volume and inter-flood period under 2030 climate suggest a latitudinal gradient of climate change impact in the basin. In the Macquarie River, average flood volume per event is projected to decrease by 25%, and inter-flood period increase by nearly 20% (CSIRO 2008). In the River Murray, best estimate model projections suggest a 45% decrease in average flood volume per event, and an increase in

inter-flood period of 13%. On the basis of the evidence presented these changes are likely to further reduce the extent of wetland grasslands in the basin but are unlikely to threaten the viability of *E. camaldulensis* forest.

Conclusions

Floodplain wetlands are a fundamental component of terrestrial landscapes, providing habitat and resources for waterbirds and woodland birds, fishes, invertebrates, reptiles and amphibians (Bino et al. 2015). It is likely that changes in vegetation structure, composition and condition will have flow-on effects to other components of the ecosystem (Bino et al. 2015). The loss of wetland grasslands is of particular concern, given the historical use of Water Couch (*P. distichum*) and Moira Grass (*P. spinescens*) by herbivorous waterfowl (Braithwaite and Frith 1969; Colloff et al. 2014) and kangaroos which preferentially feed on Water Couch in the lower Murrumbidgee wetlands (Iles et al. 2010).

Wetland managers in the Macquarie Marshes raised concerns more than a decade ago about the homogenisation of wetland plant communities: the conversion of a complex vegetation mosaic into monospecific stands of *E. camaldulensis* forest (Fazey et al. 2006). Ranchers in the Pantanal have expressed similar concerns, recalling much larger areas of grassland in former decades. They assert their right to clear woody species as a means of maintaining pasture grass, as well as maintaining biological diversity (Junk and da Cunha 2012). It is imperative that monitoring incorporate vegetation community extent mapping despite the difficulties associated with data collection and validation.

While satellite-derived canopy condition metrics (NDVI) have become a standard means of assessing floodplain wetland condition (Cunningham et al. 2011), such responses are largely ephemeral (Wen and Saintilan 2015). On the basis of the ecophysiological responses of *E. camaldulensis* during the Millennium Drought at Yanga National Park in the Lower Murrumbidgee Wetlands, many trees can survive a drought of 15 years duration, depending on soil water availability (Mayence et al. 2010). Trees that appeared dead after nine years without flooding at Yanga National Park recovered markedly after two

months of flooding in 2010 (Wen and Saintilan 2015). Our time-series mapping suggests that the decline of C₄ grasslands in the Murray-Darling Basin is, by contrast, a trend sustained through the phases of wet and dry characteristic of these rivers and is likely to be exacerbated under climate change projections for the region.

Acknowledgements Sara Karimi was supported by a Macquarie University research training fellowship. Mapping was funded by the NSW Wetland Recovery Plan and the NSW Rivers Environmental Restoration Program. Shannon Simpson contributed to aerial photograph interpretation for the Macquarie Marshes. Figure 1 was developed with the aid of the IAN Image and Video Library made available through the University of Maryland.

Funding The funding was supported by Department of the Environment, Australian Government.

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