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PRIMARY RESEARCH PAPER

Long-term changes in freshwater aquatic plant communities following extreme drought

Skye Wassens · Nathan Ning · Lorraine Hardwick · Gilad Bino · James Maguire

Abstract Prolonged periods of floodplain drying are becoming increasingly common due to severe drought events and the effects of river regulation. Using long-term monitoring, we assessed changes in freshwater plant community structure and composition before (2000–2002) and after (2010–2013) an extended drying period that resulted in two formerly persistent and three seasonally inundated wetlands in south-eastern Australia remaining continuously dry for durations ranging from 4.7 to 9.4 years. Plant community composition and structure changed significantly between pre- and post-dry stages in all wetlands. These changes were characterised by significant reductions in the percentage cover of aquatic species and the loss of formerly dominant aquatic species—in particular, the herbaceous perennial species, *Eleocharis acuta* R.Br. and *E. sphacelata* R.Br., and the aquatic grass, *Pseudoraphis spinescens* (R.Br.) Vickery. Small areas of *E. acuta* began to re-establish in the second and third years of wetland refilling, whereas *E. sphacelata* and *P. spinescens* did not re-establish and the percentage cover of aquatic species overall remained significantly below 2000–2002 levels throughout the 2010–2013 period. These results lend empirical support to our understanding of floodplain dynamics and resilience, and in particular, the loss of dominant perennial aquatic species and establishment of opportunistic annual species following extended wetland drying.

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Introduction

The modification of wetting and drying cycles of floodplains in response to river regulation and water resource development is a growing concern for the management of many floodplain aquatic plant communities (Chauhan & Gopal, 2005; Reid & Capon, 2011; Bino et al., 2015). Such hydrological changes have reduced the frequency of inundation, thereby extending the dry periods, or increased the frequency and regularity of inundation, thereby extending the wet period and increasing water level stability (Kingsford, 2000).

Extended drying due to river regulation alone or in association with drought has the capacity to alter the structure and composition of aquatic plant communities (Reid & Capon, 2011; Bino et al., 2015), and slow the rate of recovery of plant communities after inundation is restored (Brock et al., 2003). Understanding minimum water requirements (e.g. flow volumes and frequencies) below which thresholds are crossed from desired to undesired states is vital for managing for ecosystem resilience. Crossing such thresholds may significantly limit the success of future restoration actions (Groffman et al., 2006; Zweig & Kitchens, 2009).

Resilience represents the ability of an ecosystem to undergo disturbances while maintaining its basic structure and functions (Holling, 1973). Ecological resilience can be regarded as a combination of two processes: 'resistance' and 'recovery' (Côté & Darling, 2010; McClanahan et al., 2012). 'Resistance' is defined by the degree to which an ecosystem component changes following a disturbance, while 'recovery' refers to the time required for the ecosystem to return to its pre-disturbance state following the disturbance (Pimm, 1984). Empirical evidence suggests that most ecosystems can alternate among stable and functioning states depending on prevailing conditions (Beisner et al., 2003). When small disturbances shift an ecosystem from one state to another, these can be considered as threshold responses, commonly leading to substantial functional and/or compositional change (Groffman et al., 2006).

In temporary and seasonally inundated wetlands, vegetation communities transition between being characterised by wet- and dry-adapted species in response to changing water availability (Rhazi et al. 2009). The dynamic transition between wet and dry states is facilitated by two key regeneration strategies, seedbank formation and the durability of dormant seeds within the seedbank (Brock et al., 2003; Reid & Capon, 2011), and the survival of above- and below-ground vegetative propagules (rhizomes and tubers) (Combroux et al., 2001; Reid & Capon, 2011).

The same adaptations that allow for regular transitions between wet and dry communities may also facilitate recovery of aquatic communities following drying events that extend beyond the normal level of variability (Brock et al., 2003). Many, but not all, wetland species contribute to a persistent seedbank that can facilitate recovery following extended drying and thus strongly influence long-term vegetation dynamics; however, tolerances and seedbank longevity vary among species (Brock et al., 2003; Carta et al., 2013; Capon et al., 2016). Likewise, the longevity of perennial species either as a continuing part of the above-ground biomass or as below-ground propagules varies among species (Reid & Capon, 2011; Vivian et al., 2014). Flood-facilitated dispersal and colonisation can also contribute to the wetland community during the recovery phase (Boedeltje et al., 2003; Reid et al., 2016). While there is increasing interest in the mechanisms driving the resilience of aquatic vegetation communities subject to periods of extended drying, much of our understanding of the impacts of prolonged drying has been inferred from seedbank emergence trials (e.g. Brock et al., 2003; Capon & Brock, 2006). For example, Brock et al. (2003) recorded multiple species losses from the seedbank after five years of drought, while Brock (2011) and Reid & Capon (2011) showed that where species community dominants have low persistence in the seedbank, even relatively short dry periods have the capacity to fundamentally alter the composition of the community upon re-wetting. By contrast, relatively few studies have investigated vegetation re-establishment following hydrological alteration under field conditions (Alexander et al., 2008; Reid & Capon, 2011; Vivian et al., 2014). In addition, longer term datasets that allow for the assessment of changes in aquatic vegetation communities under field conditions are relatively scant, and

those that exist typically focus on a small number (less than five) of waterbodies (e.g. Ozimek & Kowalczewski, 1984; Blindow et al., 1993; Søndergaard et al., 2007).

South-eastern Australia was affected by an extreme drying event from 2001 to 2009, referred to as the 'Millennium Drought' (Dijk et al., 2013). The Millennium Drought resulted in inflows declining across the southern Murray–Darling Basin (MDB), with an average of 55% of long-term mean annual flow in the Murrumbidgee River at Wagga Wagga (Dijk et al., 2013). While droughts are a relatively common feature of Australian arid and semi-arid environments (Kirby et al., 2013), the Millennium Drought—like the 2007–2009 California drought in the USA (Aghakouchak et al., 2014)—resulted in the most persistent dry conditions and associated low river flows on record, with its impacts on natural environments exacerbated by high rates of water extraction and diversion. The Millennium Drought was preceded by a period of significant water resource development and expansion of irrigated agriculture, which had already contributed to widespread declines in the condition and extent of downstream floodplain wetlands (Kingsford, 2003; Kandasamy et al., 2014). The combination of reduced water availability due to low catchment rainfall and increasing irrigation and consumptive demand, resulted in a period of very low riverine water levels, and consequently wetlands that relied on lateral connection with the river during flow peaks became disconnected and dried. The drought ended in 2010, when a period of high rainfall triggered widespread flooding events throughout south-eastern Australia. The end of the drought, coupled with significant water reforms, facilitated the restoration of water flows into lower lying wetlands between 2010 and 2013 (Kandasamy et al., 2014).

In this study, we quantify and compare the composition and structure of aquatic vegetation species in five temperate Australian floodplain wetlands, before and after the prolonged drying period associated with the Millennium Drought and accompanying protracted period of low river flow. Our study focuses on waterbodies historically classified as permanent and semi-permanent (seasonally inundated), with aquatic vegetation communities representative of open, grassy aquatic meadows (Colloff et al., 2014) and a fringing riparian overstory comprising River Red Gum (*Eucalyptus camaldulensis* Denhn.) (Chessman & Hardwick

2014). We monitored the aquatic community composition and structure using repeat sampling over a two-year period (2000–2002) prior to wetland drying and then again over a three-year period between 2010 and 2013 after the wetlands had refilled. Detailed vegetation data collected prior to wetland drying, coupled with monitoring of wetlands that had been disconnected for differing periods, provided an opportunity to examine changes in the composition and structure of wetland aquatic vegetation communities following exposure to extended drying events, measure their recovery following refilling, and thus evaluate the impact of duration of drying on the resilience of these communities.

Materials and methods

Study area

The study was undertaken in the mid-Murrumbidgee River region in the southern MDB in south-eastern Australia (34°42′S, 146°25′E). The Murrumbidgee River rises in the Snowy Mountains and flows west for around 1600 km, before discharging into the Murray River near Balranald. Its mean annual discharge of 3890 GL at Wagga Wagga is highly regulated by two storage structures: Burrinjuck Dam on the Murrumbidgee River and Blowering Dam on the Tumut River, a tributary that meets the Murrumbidgee upstream of Wagga Wagga (Green et al., 2011). Average annual rainfall is 432 mm at Narrandera (1967–2015) in the southern region of the study area, and 367 mm at Hay (1877–2015) in the western region (Australian Bureau of Meteorology, 2016).

In south-eastern Australia, inland lowland floodplains are characterised by an extensive overstory of River Red Gum communities. River Red Gum communities can tolerate periods of inundation when mature, but are excluded from areas of frequent (seasonal) inundation, giving way to open grassy aquatic meadows (Roberts & Marston, 2011). The mid-Murrumbidgee floodplain features a complex series of deep meander scars and anabranches associated with a series of open wetlands, with fringing River Red Gums. Wetlands are connected to the main river channel during flow peaks, and consequently the regulation of river flows, particularly the reduction in higher flow peaks through water regulation and

upstream diversion, has had a significant impact on the hydrology of wetlands in this system (Page et al., 1996).

Study design

We repeatedly surveyed aquatic plant communities in the five floodplain wetlands, Berry Jerry (BEJ), Molleys (MOL), Sunshower (SUN), Yarradda (YAR) and McKennas (MCK) (Table 1), from 2000 to 2002 as part of the Integrated Monitoring of Environmental Flows (IMEF) program (Chessman, 2003), and then again from 2010 to 2013 after widespread flooding refilled all five wetlands (see Table 1). Three wetlands (SUN, YAR and MCK) were wide oxbow lagoons, with moderate edge profile (slope) and a depth:width ratio less than 0.01, while MOL and BEJ were narrower and more steeply incised with a depth:width ratio greater than 0.01 (Table 1). All five wetlands are close to the river and reconnect at least annually during high winter and spring flows under typical conditions (Page et al., 1996). After

these wetlands have been connected to the river during high winter/spring flows, their hydroperiods range from 6 to 18 months (see Table 1), meaning that larger wetlands, while often undergoing seasonal drawdown, rarely if ever dry completely.

In each wetland, aquatic vegetation communities were repeatedly sampled at set intervals (1, 3, 5 and 7 months) following wetland inundation in the Austral spring–autumn months through the 2000–2001 and 2001–2002 water years (July 1–June 30), and then routinely four times per year in October, December, February and April of 2010–2011, 2011–2012 and 2012–2013. The IMEF sampling protocol did not include surveys of wetlands in their dry phase, so although monitoring between 2010 and 2013 continued during subsequent dry phases, we only included data from surveys conducted during periods when the wetlands contained water to match the sampling protocols for the pre-dry IMEF surveys.

In each wetland, we established three transects that ran from the high water mark to a point 100 m into the wetland or to the opposite high water mark depending

Table 1 Study sites and hydrological characteristics

Variable	Wetland[a]				
	Berry Jerry	Molleys	Sunshower	Yarradda	McKennas
Latitude	35°1′1.43.00″S	34°43′24.02″S	34°36′39.59″S	34°34′20.61″S	34°25′28.68″S
Longitude	147°3′52.58″E	146°20′29.96″E	146°1′13.10″E	145°48′54.93″E	145°30′54.10″E
Vegetation classification[b]	OF	OF	GAM	GAM	GAM
Months dry[c]	57	73	113	97	107
Longest period wet (months)[d]	36 (2000–2003)	36 (2000–2003)	8 (2000–2001)	18 (2000–2002)	18 (2000–2002)
Mean duration retains water (months)	12	18	7	19	14
Depth:width ratio (m)	3.5:80 (0.044)	1.2:36 (0.033)	1.2:180 (0.007)	1.2:280 (0.004)	2:250 (0.008)
CTF gauge level (m)	3.2	5.13	4.24	4.24	4.18
Gauge name	Wagga Wagga	Narrandera	Darlington Point	Darlington Point	Carrathool
1974–1993 mean number of days connected to the river annually	66.1 ± 57.8SD	45.8 ± 48.9SD	55.8 ± 55.3SD	55.8 ± 55.3SD	Not available
1994–2009 mean number of days connected to the river annually	26.6 ± 25.7SD	4.6 ± 11.1SD	6.2 ± 13.1SD	6.2 ± 13.1SD	Not available

CTF commence-to-fill

[a] *BEJ* Berry Jerry Lagoon (20 surveys), *MOL* Molleys Lagoon (13 surveys), *SUN* Sunshower Lagoon (15 surveys), *YAR* Yarradda Lagoon (14 surveys), *MCK* McKennas Lagoon (17 surveys)

[b] *OF* open fringing, *GAM* grassy aquatic meadow (Chessman, 2003)

[c] For 2000–2013

[d] For 2000–2010 (year range)

on which was closer. The same transects were then sampled repeatedly for the duration of the study. Each transect was positioned perpendicular to the edge of the wetland from the high water mark through the cross-sectional mid-point of the wetland. During the IMEF program, we sampled vegetation in 1 m^2 quadrats every metre along each 100-m transect or to the opposite high water mark, which resulted in 70–100 quadrats per transect. During the post-dry monitoring we sampled 1 m^2 quadrats every three metres along the same transect (thirty 1 m^2 quadrats per transect). To standardise sampling effort between pre- and post-dry surveys, we subsampled the pre-dry surveys to produce thirty 1 m^2 quadrats per transect for each survey. It was not appropriate to randomly subsample the IMEF transects, because the random subsamples would not have matched the post-dry sampling design. Rather, to consolidate the two survey methods, we subsampled the IMEF transect data at the same set 3-m interval as that applied in the 2010–2013 transects, to produce three transects each containing thirty 1 m^2 quadrats, resulting in ninety 1 m^2 quadrats per wetland for each sampling occasion across all water years. Plants were identified to species level wherever possible in accordance with Sainty & Jacobs (2003) and names were validated against the NSW Plant Information Network System (PlantNET, 2014). Each plant was assigned to aquatic functional group according to Brock and Casanova (1997) (Table A1, Appendix 1).

Fine-scale wetting and drying regimes of each wetland from 1999 until around 2006 were drawn from depth loggers and gauge plate readings where available (NSW Office of Water) and wetland depth observations during surveys between 2010 and 2013. We estimated the long-term hydrological regime of wetlands of the Murrumbidgee floodplain complex based on their elevation above the river, which is the elevation (or discharge rate) where the inflow channel connects with the main river channel (i.e. commence-to-fill (CTF) height). We then derived the long-term inundation pattern for each wetland by calculating the number of days where the relevant river gauge water height (Department of Primary Industries Water, 2016) exceeded its CTF height. To assess hydrological change between the 1974–1993 and 1994–2014 periods, we fitted a generalised linear model, assuming Poisson distribution, of the relationship between the number of days above CTF height and period using the

GLM function in R (R Development Core Team, 2014).

Data analysis

To investigate the response and recovery of wetland aquatic plant communities following exposure to extended drying, we compared patterns using data on mean percentage cover per quadrat per transect for four dry stages: pre-dry (2000–2002), immediately post-dry (2010–2011), one-year post-dry (2011–2012) and two-year post-dry (2012–2013). We used a generalised additive model (GAM) assuming beta distribution of errors to test for variation in the proportion of total vegetation cover incorporating both the 'dry stage' ($n = 4$) and 'site' ($n = 5$) as explanatory factors. We also used a GAM assuming beta distribution of errors to test for variation in vegetation cover of three particular taxa (*Eleocharis* spp*., Centipeda cunninghamii,* (DC.) A.Braun & Asch and *Alternanthera denticulate* R.Br.), by incorporating 'species' ($n = 3$), 'dry stage' ($n = 4$), and 'site' ($n = 5$) as explanatory factors. We modelled responses using the 'mgcv' package (Wood & Wood, 2016) and undertook post hoc interaction analysis using the 'phia' package (De Rosario-Martinez, 2015) in R (R Development Core Team, 2014).

Multivariate community analyses, derived from Bray–Curtis similarity matrices, were undertaken to examine dry-stage and wetland (i.e. site)-related variation in aquatic plant community structure (i.e. community patterns attributed to the relative abundance of taxa) and community composition (i.e. community patterns attributed to the presence or absence of taxa), using arcsine square-root and presence–absence transformed percentage cover data, respectively (Ning et al., 2011). Assessments of the relative magnitude of community change among dry stages for each wetland and the relative directions of these changes were undertaken using Non-metric Multidimensional Scaling plots (NMDS in Primer V6.0 (Clarke & Warwick, 2001)), based on distances among centroids. The NMDS patterns were then formally examined using two-way repeated measures PERMANOVA [PERMANOVA + for Primer] (Anderson, 2005; Anderson et al., 2008) with wetland as a between-group fixed factor and dry stage as a within-group fixed factor. Taxa contributing most to variation among communities were assessed using the similarity percentages

procedure (SIMPER in Primer V6.0 (Clarke & War-wick, 2001)). SIMPER analyses were performed on community structure to establish which species contributed to 90% of the dissimilarity between the pre- and immediately post-dry stage communities in each wetland. To assess changes in the similarity of plant communities to their pre-dry forms over time, we compared Bray–Curtis similarities in plant communities between the pre-dry (i.e. 2000–2002) and immediately post-dry (i.e. 2010–2011) stages with those between the pre-dry and one-year post-dry (i.e. 2011–2012) stages, and the pre-dry and two-year post-dry (i.e. 2012–2013) stages for each wetland. We undertook a two-way PERMANOVA, with dry stage comparison (e.g. pre-dry vs immediately post-dry) and wetland as fixed factors to formally assess these changes in community similarity through time. The two-way PERMANOVA analyses were again done for both aquatic plant community structure and community composition, using arcsine square-root and presence–absence transformed percentage cover data, respectively.

Species richness (S) was calculated for each survey at each site using Primer V6.0. Kruskal–Wallis test by ranks was used to compare median species richness across the four dry stages: pre-dry (2000–2002), immediately post-dry (2010–2011), one-year post-dry (2011–2012) and two-year post-dry (2012–2013).

Results

Long-term inundation patterns

To illustrate long-term inundation patterns for each wetland in the absence of more detailed hydrological data, we used a simple metric of the proportion of days where the commence-to-fill threshold was exceeded during each decade to quantify the change in water availability. Gauge data were not available for MCK until 1996. Through the 1970s, 1980s and early 1990s, there were regular inflows into the wetlands, resulting in YAR, SUN and MOL being classified as seasonally inundated with periodic drying, and BEJ being classified as permanent (Table 1). During the late 1990s to 2010, a major reduction in the frequency of river-wetland connections occurred, with inflows declining to less than 5% of the long-term average for 1970–2000 at YAR, SUN and MOL, and 25% of

the long-term average at BEJ (Table 1; Fig. 1). Between 1994 and 2014, wetlands were subjected to dry periods that far exceeded the 1974–1993 average proportion of days above commence-to-fill threshold ($P < 0.001$) (Fig. 1), although there was still a high level of variability in the combined effects of the dry periods and river regulation on their hydrological regimes. BEJ remained the most frequently reconnected, but experienced fewer connections from 2006 to 2010. SUN was frequently connected up until mid-2000 and dried by early 2001, receiving just one brief connection in spring 2005 before becoming dry again by early 2006. YAR was also frequently connected prior to 2001, and dried completely by early 2002. It experienced a partial fill at the end of 2005 and was dry again by early 2006. MOL retained water until early 2003, briefly reconnected in 2005 and dried by mid-2006, while MCK was seasonally connected up until 2001 (Fig. 1) before it dried early in 2002 and remained so until 2010.

Aquatic plant communities

Aquatic plant cover, community structure and composition were all greatly altered following exposure to extended drying. In total, 51 species were recorded from across the five sites (Table A1, Appendix 1). Species richness was similar between the pre- (2000–2002) (38) and post-dry (2010–2013) (39) periods, while 26 species were identified during both periods. Thirty of the 51 species were classified as belonging to the amphibious functional groupings (Brock & Casanova, 1997), with 26 of those species recorded in the pre-dry period and 18 of those species recorded in the post-dry period. The remaining 21 species fell into the Terrestrial Damp functional group (i.e. plants that colonise mud-flats and damp areas, but that are not tolerant of extended periods of water logging). There were more of these species recorded during the post-dry period (21 species) than during the pre-dry period (12 species).

During the pre-dry period, wetland communities were characterised by four key herbaceous perennial aquatic species: *Eleocharis acuta* R.Br (mean % cover 16.2 ± 24.8SD), *Eleocharis sphacelata* R.Br. (mean % cover 3.1 ± 5.5SD), *Ludwigia peploides* ssp. *montevidensis* (Spreng.) (mean % cover 1.3 ± 3.5SD) and the aquatic grass, *Pseudoraphis spinescens* (R.Br.) Vickery (mean % cover 3.0 ± 4.4SD) (Table 2). Immediately
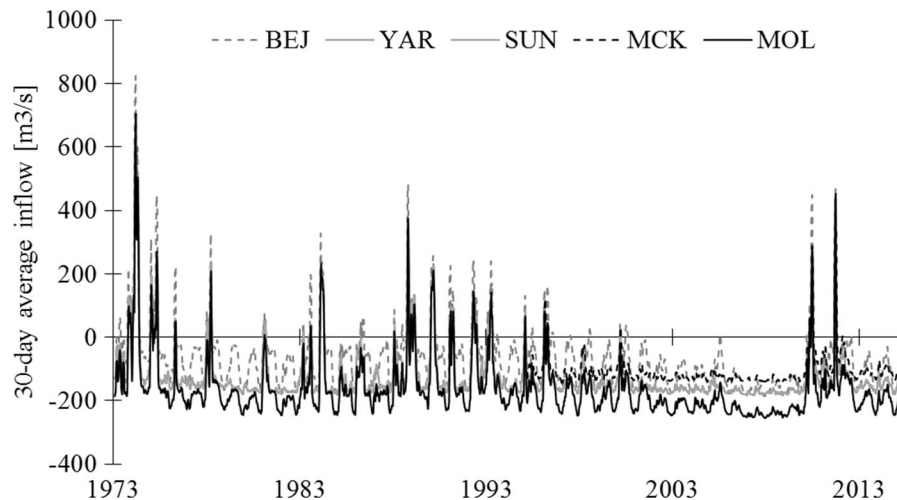
Fig. 1 Thirty-day average cumulative inflows. Days where river discharge levels were above (positive values) or below (negative values) the commence-to-fill (CTF) threshold (represented by the discharge level of 0 m³ s⁻¹) for each wetland from 30 June 1970 until 1 July 2015. See Table 1 for CTF levels. For the wetlands, *BEJ* Berry Jerry, *MOL* Molleys, *SUN* Sunshower, *YAR* Yarradda, *MCK* McKennas. Note that data are only available for the Carrathool Gauge (MCK) from 1996

post-dry, the percentage cover of *Eleocharis* spp. had significantly decreased from a mean % cover of 20.8 ± 25.0SD to 0.1 ± 0.2SD ($\chi^2 = 142.48$, $P < 0.001$), but recovered slightly at one-year post-dry ($\chi^2 = 67.08$, $P < 0.001$) and two-year post-dry (4.3 ± 7.1SD, $\chi^2 = 40.75$, $P < 0.001$) (Table A2, Appendix 1). Of the *Eleocharis* species, *E. acuta* began to slightly recover in each wetland by the first and second years of post-dry, whereas *E. sphacelata* remained absent (Table 2). Also, *Pseudoraphis spinescens* was relatively abundant in the pre-dry samples (mean % cover 3.0 ± 4.4SD), but remained absent from all five wetlands during the post-dry period (Table 2). In contrast, there were significant increases in the cover of the annual forbs, *Alternanthera denticulata* and *Centipeda cunninghamii*. *Alternanthera denticulata* increased in cover immediately post-dry ($\chi^2 = 6.65$, $P = 0.009$), before increasing further in cover one-year post-dry ($\chi^2 = 64.28$, $P < 0.001$) and remaining relatively high in cover two-years post-dry ($\chi^2 = 25.76$, $P < 0.001$), (Table A4, Appendix 1), while *Centipeda cunninghamii* did not increase in cover immediately post-dry ($\chi^2 = 0.82$, $P = 0.36$), but significantly increased one-year post-dry ($\chi^2 = 12.96$, $P < 0.001$), and further increased in cover two-years post-dry ($\chi^2 = 23.54$, $P < 0.001$), (Table A4, Appendix 1).

The proportion of total vegetation cover was significantly reduced between the pre-dry

(2000–2002) and immediately post-dry (2010–2011) stages ($\chi^2 = 81.33$, $P < 0.001$) (Table A2, Appendix 1). This re-wetting period was followed by a significant increase in the proportion of total vegetation cover in subsequent years (one-year post-dry 2011–2012: $\chi^2 = 15.94$, $P < 0.001$, two-years post-dry 2012–13: $\chi^2 = 8.85$, $P = 0.003$) (Table A2, Appendix 1). Prior to drying, the percentage cover of aquatic species was greater than 20% in four of the five wetlands (BEJ, YAR, SUN, MCK) (mean $29.77\% \pm 25.58$SD), whereas the percentage cover of aquatic species was reduced to an overall average of $2.7\% \pm 1.55$SD immediately post-dry. The most significant change in aquatic vegetation cover occurred at SUN, where cover decreased from 72.7% pre-dry to 1.7% immediately post-dry (2010–2011; $\chi^2 = 109.33$, $P < 0.001$) (Table 2). Over the following two years after the first refilling (one- and two-years post-dry), vegetation cover increased slightly in four of the wetlands, but remained at less than half of its pre-drying level at BEJ and SUN. At MOL, the total percentage cover of aquatic vegetation generally increased over time, but remained at less than 10% throughout the study (Table 2).

The variation in plant community structure and composition between pre- and post-dry stages was significant in all wetlands (PERMANOVA; Table 3), except in a few comparisons where the variation was at most only marginal for BEJ and MOL (Fig. 2). The

Table 2 SIMPER analysis using percentage cover (arcsine square-root transformed data) of the species contributing to 90% of the dissimilarity between the pre-dry and immediately post-dry stage at each wetland (dominant species only)

Wetland	Species	Contribution%	Mean cover (%)			
			P	0	1	2
BEJ	Eleocharis acuta	20.07	6.9	0.06	1.07	1.31
	Ludwigia peploides ssp. montevidensis	18.59	6.59	0.00	0.06	0.00
	Eleocharis sphacelata	16.48	6.83	0.20	0.50	1.17
	Carex bichenoviana	9.59	3.26	0.00	0.00	0.00
	Juncus usitatus	7.76	0.56	1.49	0.08	0.53
	Paspalidium jubiflorum	5.19	0.80	0.38	2.70	2.79
	Pseudoraphis spinescens	3.99	0.54	0.00	0.00	0.00
	Total mean percentage cover		26.3[a]	3.68[b]	6.45[ab]	6.78[ab]
MOL	Persicaria prostrata	34.79	0.00	1.62	1.59	0.99
	Alternanthera denticulata	12.83	0.00	0.74	0.43	0.03
	Alternanthera nana	9.9	0.00	0.58	0.19	0.00
	Centipeda cunninghamii	8.55	0.00	0.51	0.19	0.25
	Carex inversa	7.36	0.00	0.34	1.69	2.03
	Eleocharis acuta	5.01	0.08	0.00	0.27	0.56
	Pseudoraphis spinescens	4.66	0.06	0.00	0.00	0.00
	Total mean percentage cover		0.2[a]	4.09[b]	8.49[c]	7.34[c]
SUN	Eleocharis acuta	67.56	62.5	0.12	6.84	12.7
	Pseudoraphis spinescens	8.03	4.4	0.00	0.00	0.00
	Eleocharis pusilla	6.8	1.1	0.00	2.09	4.01
	Eucalyptus camaldulensis	4.51	1.56	0.79	0.59	0.32
	Alternanthera denticulata	3.37	0.00	0.43	4.11	1.88
	Total mean percentage cover		72.7[a]	1.66[b]	15.9[a]	24.4[a]
YAR	Eleocharis acuta	30.33	8.67	0.11	0.56	1.11
	Eleocharis pusilla	19.46	6.13	0.00	0.00	0.00
	Pseudoraphis spinescens	16.05	4.79	0.00	0.00	0.00
	Eucalyptus camaldulensis	11.48	0.00	1.17	0.47	0.82
	Centipeda cunninghamii	4.1	0.79	0.01	4.04	3.46
	Alternanthera nana	0.00	0.00	0.13	0.00	0.00
	Paspalidium jubiflorum	2.91	0.17	0.34	1.3	1.36
	Total mean percentage cover		21.3[a]	1.84[b]	14.5[ac]	13.4[ac]
MCK	Phyla canescens	26.2	10.9	0.00	0.58	0.00
	Pseudoraphis spinescens	17.96	4.99	0.00	0.00	0.00
	Eleocharis sphacelata	13.69	6.03	0.00	0.00	0.00
	Eleocharis acuta	12.27	3.09	0.00	0.16	0.28
	Eucalyptus camaldulensis	11.19	0.00	1.81	2.16	2.51
	Azolla pinnata	4.32	0.91	0.00	0.00	0.00
	Triglochin procera	4.11	0.83	0.00	0.04	0.03
	Total mean percentage cover		28.3[a]	1.96[b]	9.1[c]	16.6[c]

Contribution% is the proportion of dissimilarity between the pre-dry (2000–2002) and immediately post-dry stage (2010–2011) communities contributed by each species at each wetland. Superscript letters have been included with total percentage covers to show where there were significant differences between dry stages for each wetland. P pre-dry, 0 = immediately post-dry, 1 = one-year post-dry (2011–2012) and 2 = two-years post-dry (2012–2013). See Table 1 for an explanation of the site acronyms

overall temporal trajectories of community change were similar in each wetland, with community structure and composition least similar to their pre-dry forms immediately post-dry (Fig. 3). Despite the alterations to aquatic plant community structure, composition and cover following extended drying, there was some evidence of a trend towards becoming increasingly similar to their pre-dry forms during the one- and two-year post-dry stages, but the trend was very weak (Figs. 2, 3, 4). Specifically, pre-dry versus post-dry similarities in plant community structure and composition increased from immediately post-dry to one-year post-dry, but then remained similar in subsequent drying stages (Fig. 4). An exception occurred at MOL, where the pre-dry versus post-dry similarity in plant community structure did not increase greatly from immediately post-dry to two-years post-dry (Fig. 4). PERMANOVA confirmed that the pre-dry versus post-dry similarities in plant community structure and composition both varied significantly among dry stages and wetlands, and that there was an interaction between the effects of dry stage and wetland on community structure (Table 4; Fig. 4).

The plant communities in wetlands that had been subjected to longer dry periods did not recover towards their pre-dry forms to the same extent as the plant communities in wetlands that had been subjected to shorter drying periods (Fig. 4). During the one- and two-year post-dry stages, plant community structure and composition at MCK remained consistently less similar to their respective pre-dry forms compared to the communities at BEJ, SUN and YAR. Indeed, overall similarities in pre- versus post-dry community composition were greatest at BEJ, SUN and YAR, followed by at MCK, and then at MOL (Fig. 4).

Fig. 2 Two-dimensional NMDS solutions based on distances among centroids for the mean percentage cover of all aquatic plant taxa according to dry stage and wetland. Ordinations are presented to show patterns for aquatic plant community structure (arcsine square-root transformed percentage cover data (**a**)) and community composition (presence–absence transformed percentage cover data (**b**)). P = pre-dry (2000–2002), 0 = immediately post-dry (2010–2011), 1 = one-year post-dry (2011–2012) and 2 = two-years post-dry (2012–2013). See wetland codes in Fig. 1

PERMANOVA confirmed that the consistent wetland differences in plant community composition were significant (all wetland comparison differences were significant except for those between BEJ, SUN and YAR) (Table 4; Fig. 4).

Table 3 Pseudo-F ratios and significance levels for PERMANOVA investigating the effects of wetland and drying stage on aquatic plant community structure (CS) (arcsine square-root transformed percentage cover data for all of the taxa within a community), community composition (CC) (presence–absence transformed percentage cover data for all of the taxa within a community) and percentage cover (% cover) (arcsine square-root transformed data for the total percentage cover)

Source	df	CS	CC	%cover
Wetland	4	10.771**	9.741**	16.084**
Drying stage	3	13.971**	14.548**	35.278**
Wetland x Drying stage	12	3.420**	2.018**	7.228**

Drying stages consisted of pre-drying (2000–2002), immediately post-dry (2010–2011), one-year post-dry (2011–2012) and two-years post-dry (2012–2013)
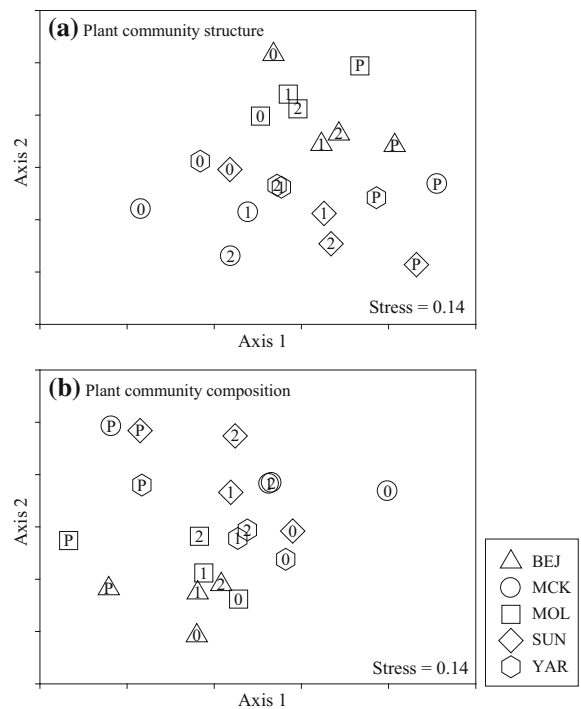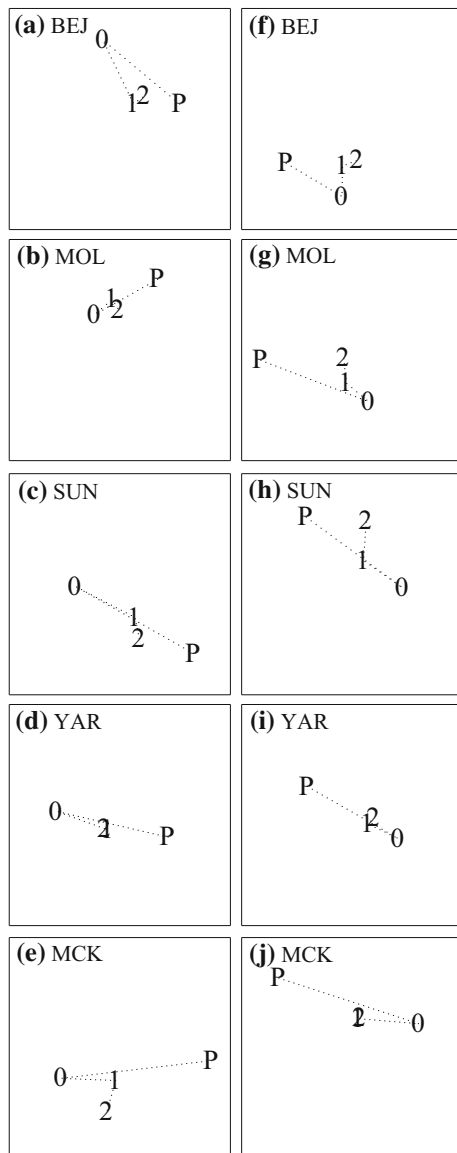
** $P < 0.01$

Fig. 3 Temporal trajectories in terms of total aquatic plant community structure (arcsine square-root transformed percentage cover data (a–e)) and community composition (presence–absence transformed percentage cover data (f–j)) in each wetland. The trajectories have been taken from the plant community structure and community composition NMDSs (Fig. 2), and displayed separately for each wetland to improve clarity (stress = 0.14 for each NMDS). See wetland codes in Fig. 1 and dry stage codes in Fig. 2
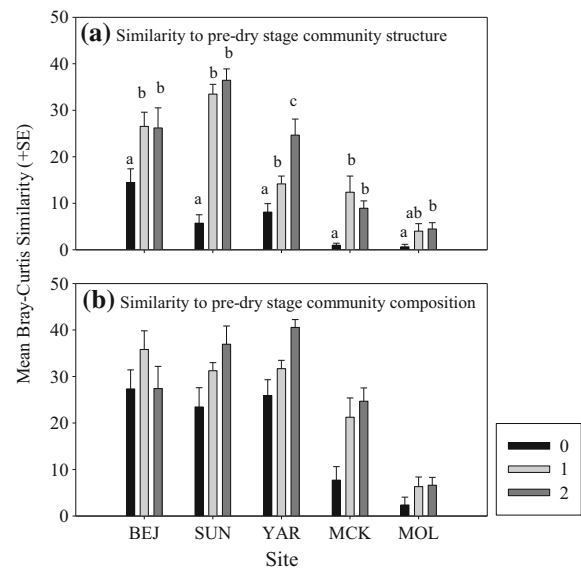

Fig. 4 Average Bray–Curtis similarity in a community structure (arcsine square-root transformed percentage cover data) and b community composition (presence–absence transformed percentage cover data) between post-dry stages (0, 1 and 2) and the pre-dry stage (P) in each wetland (n = 9). There was a significant interaction between the influence of wetland and dry stage comparison for community structure (Table 2), and thus, the letters have been included above each bar to show where there were significant differences between dry stage comparisons for each wetland. For each wetland, dry stage comparisons sharing the same letter do not significantly differ in terms of their average Bray–Curtis similarity in community structure. See wetland codes in Fig. 1 and dry stage codes in Fig. 2

mean 0.75 ± 0.10SE), immediately post-dry (0.59 ± 0.11), one-year post-dry (0.95 ± 0.03) and two-year post-dry (0.89 ± 0.04) stages (Kruskal–Wallis 7.621, $P = 0.055$). The pattern of species richness change varied considerably among sites. Species richness differed between pre- and post-dry samples at MCK (Kruskal–Wallis 9.839, $P = 0.020$) and SUN (Kruskal–Wallis 8.751, $P = 0.033$), but not at MOL (Kruskal–Wallis 5.073, $P = 0.167$), YAR (Kruskal–Wallis 6.338, $P = 0.096$) or BEJ (Kruskal–Wallis 0.710, $P = 0.871$) (Fig. 5). Only MCK showed the expected pattern of a decline in species richness immediately post-dry and a gradual recovery in the following two years (Fig. 5).

Discussion

Globally, increasing water demands coupled with an increasing intensity and severity of drought events will

Wetland species richness

When considered across the five wetlands, there was a slight, but non-significant difference in site-scale species richness (S) between the pre-dry (Log10 S

Table 4 Pseudo-*F* ratios and significance levels for PERMA-NOVA investigating differences in average Bray–Curtis similarity in community structure (CS) (arcsine square-root transformed percentage cover data for all of the taxa within a community), and community composition (CC) (presence–absence transformed percentage cover data for all of the taxa within a community) between pre- and post-drying stage comparisons at each site

Source	df	CS	CC
Wetland	4	38.237**	40.401**
Drying stage comparison	2	44.968**	20.729**
Wetland × Drying stage comparison	8	4.490**	1.768

Drying stage comparisons consisted of pre-drying (2000–02) vs. immediately post-dry (2010–2011), pre-drying vs. one-year post-dry (2011–2012), and pre-drying vs. two-year post-dry (2012–2013)

** $P < 0.01$

have a profound impact on freshwater communities (Palmer et al., 2008). Multiple studies have shown that drought can change the structure and function of vegetation communities (e.g. Vicente-Serrano et al., 2013; Garssen et al., 2014; Capon et al., 2015). Throughout much of the world, the effects of severe drought occur in the context of already-high levels of anthropogenic disturbance and modification, making it difficult to decouple the role of climate variability and ongoing flow modification (Palmer et al., 2008). In the mid-Murrumbidgee River region where this study

Fig. 5 Mean (±1 SE) species richness (Log10 transformed) (*n* = 3) during the pre- and post-dry stages in each wetland. See wetland codes in Fig. 1 and dry stage codes in Fig. 2

was undertaken, it is important to note that while the drought was severe, the impacts of flow regulation during this period played a key role in reducing inundation (Dijk et al., 2013). In other parts of the Murrumbidgee where the impacts of regulation were less severe, herbaceous perennial rushes (*Eleocharis* spp.) recovered rapidly upon refilling of wetlands (Reid & Capon 2011), highlighting the critical role that water management can play in mitigating the impacts of severe drought associated with climate and land use change.

Broadly, upon re-wetting there were significant reductions in the percentage cover of aquatic grassy meadow species, in particular the aquatic grass *P. spinescens* and the rushes *Eleocharis* spp. The three wetlands that recorded high (>50%) percentage cover of aquatic vegetation prior to drying generally showed a greater degree of change than those with lower initial cover. This pattern was largely driven by the loss of *P. spinescens* and *Eleocharis* spp., which had contributed a high proportion of the above-ground cover prior to the drought. Despite the reductions in the percentage cover of aquatic species, species richness did not change overall, largely due to the addition of opportunistic annual forbs at wetland margins. We were unable to include an assessment of the change in cover of terrestrial species because matching data were not available for the pre-drought period. However, we did record an increase in the cover of seedlings of the dominant overstory species, *Eucalyptus camaldulensis*. Mature *Eucalyptus camaldulensis* can tolerate periods of inundation, but seedlings cannot tolerate submersion; thus, frequent inundation prevents seedling establishment within wetlands and supports the establishment of open aquatic grassy meadows (Bren, 1992). In Australia, *Eucalyptus camaldulensis* encroachment
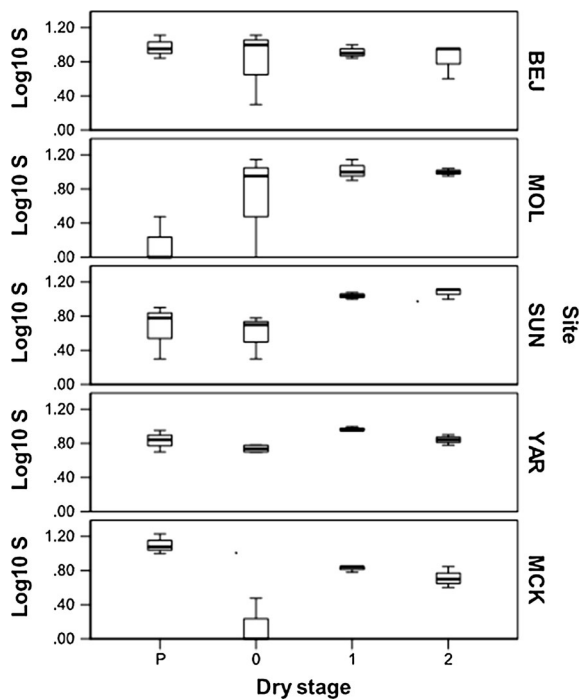
into wetlands commonly occurs in situations where the frequency of inundation has been reduced, and is currently considered to be a significant environmental problem (Saintilan & Rogers, 2015).

By the first and second years of post-dry, the percentage cover of the rush, *E. acuta*, had increased although its cover remained very low compared to its cover during the pre-drying stage, whereas *E. sphacelata* and *P. spinescens* remained absent from wetlands where they had formerly been dominant taxa. In similar communities present in the lower Murrumbidgee floodplain, *E. sphacelata* exhibited rapid surface growth upon re-wetting (Reid & Capon, 2011) so its absence during the years following re-wetting suggests that rhizomes were no longer viable.

Increases in plant cover over the years following re-wetting were largely due to the increased cover of opportunistic annual species, in particular *Centipeda cunninghamii*, *Alternanthera denticulata* and *Alternanthera nana* R.Br. These species were more abundant following refilling than they had been during the pre-dry sampling period. Nielsen et al. (2013) showed a similar dominance by these annual forb species in seedbank emergence trials using sediments from wetlands that had been dry for either two or seven years. This finding suggests that even after a relatively brief period of drying, the formerly dominant species, *Eleocharis sphacelata* and *Pseudoraphis spinescens,* were no longer viable in the form of dormant seeds or rhizomes, or that they are not a major contributor to persistent seedbanks (e.g. Colloff et al., 2014). In the case of *P. spinescens,* which is known to produce a large numbers of seeds, but with potentially limited seed dormancy, growth from vegetative propagules may be more important than germination from the seedbank in some situations (Colloff et al., 2014). Loss of *P. spinescens* in response to reduced inundation frequency is consistent with observations from other grassy wetland systems in south-eastern Australia (Colloff et al., 2014; Vivian et al., 2014).

The absence of any significant changes to overall species richness between the pre- and post-dry phases was in line with the findings from several other similar studies, including Capon & Reid (2016) and Lite et al., (2005) (for woody species). During dry periods, new communities develop within wetlands, and these communities are often dominated by species from the terrestrial dry and terrestrial damp functional groups that can grow successfully on rainfall alone

(Rhazi et al., 2009; Bino et al., 2015). When wetlands refill, species that occurred during the dry phase may remain, and form part of the post-dry community (Rhazi et al., 2009). The establishment of dry phase species along wetland margins after refilling can potentially mask the loss of sensitive aquatic species. Thus, changes in species richness need to be treated with caution when evaluating the recovery of wetland plant communities following extended drying.

In this study, two issues hampered our ability to statistically evaluate the relationship between wetland drying period and changes in vegetation structure and composition—namely the small number of wetlands considered, and the differing natural flow and hydrological regimes and geomorphologies of each site. Despite these limitations, however, this long-term dataset has provided valuable insight into the impact of extended drying on formally dominant perennial aquatic species that are often poorly represented in seedbanks. Indeed, long-term field studies offer the potential for direct analyses, in contrast to seedbank studies, which often rely on a space-for-time substitution (e.g. Nielsen et al., 2013; Capon & Reid, 2016). Nonetheless, the use of seedbank studies in conjunction with long-term field studies in the future would aid in supplying information about why certain species are not maintained after drought (e.g. those that depend on re-sprouting from rhizomes). The current study has provided a far clearer picture of the recovery potential of the formally dominant perennial species (*E. sphacelata, E. acuta*), which tend to be underrepresented in soil seedbank studies largely because of their relatively high dependence on rhizomes for re-establishment (e.g. Amiaud & Touzard, 2004). Our results also highlight the importance of considering dominant perennial species that shape community composition and structure and drive the characteristics of the vegetative response immediately following re-wetting. In seasonally inundated wetlands, the contribution of perennial species that survive drying as rhizomes or tubers to the initial biomass response following inundation may be far greater than germination from the seedbank, with the seedbank contributing more to community diversity in the months after initial inundation has occurred (Reid & Capon, 2011). The role of perennial species with dormant propagules in driving aquatic vegetation responses and resilience requires further attention.

Conclusion

Floodplain aquatic vegetation communities in many parts of the world are being increasingly subjected to prolonged periods of drying due to a rise in the occurrence of severe drought events and the effects of river regulation; yet, there is still much uncertainty regarding the resilience of such communities to extended drying events. In this study, we noted a loss of community dominants (herbaceous perennial species) following an extended drying event, which had a disproportional impact on the rate of community recovery. Although we did not specifically set up the initial vegetation surveys to test resilience in aquatic plant communities, our results provide insights into the mechanisms of aquatic plant community dynamics following extended drying and support models for floodplain resilience proposed by Colloff & Baldwin (2010). The trajectories of all five wetland plant communities showed evidence of species loss following extended drying, with some evidence of recovery after re-flooding. However, this recovery was largely driven by widespread, opportunistic species with long-lived seedbanks available to colonise mud-flats and wetland margins, while the amphibious herbaceous perennial species that previously defined the character of these wetlands were either missing entirely or occurred in very low abundances.

There are currently limited data available to define acceptable recovery rates in wetland systems as well as what constitutes a resistant and resilient floodplain community (Lake, 2013). In wetland systems already impacted by high levels of regulation and hydrological modification, quantification of the drying tolerances (i.e. resistance) of structurally dominant and functionally important species may improve our capacity to develop long-term water management strategies aimed at increasing resilience.

Under current climate change predictions, where extreme drying events are expected to become more frequent (Chiew et al., 2011), shifts from specialised-species-based aquatic communities towards opportunistic-species-based aquatic communities may become more common. Such shifts are likely to directly impact upon the ecological functioning of wetlands through changes to primary productivity, nutrient cycling, food and habitat provision (Zedler & Kercher, 2004). Long-term monitoring studies of aquatic vegetation that encompass multiple drying and wetting phases will be needed to assess these ecological changes and to improve our understanding of them.

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