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Continental impacts of water development on waterbirds, contrasting two Australian river basins: Global implications for sustainable water use

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Abstract

The world's freshwater biotas are declining in diversity, range and abundance, more than in other realms, with human appropriation of water. Despite considerable data on the distribution of dams and their hydrological effects on river systems, there are few expansive and long analyses of impacts on freshwater biota. We investigated trends in waterbird communities over 32 years, (1983–2014), at three spatial scales in two similarly sized large river basins, with contrasting levels of water resource development, representing almost a third (29%) of Australia: the Murray–Darling Basin and the Lake Eyre Basin. The Murray–Darling Basin is Australia's most developed river basin (240 dams storing 29,893 GL) while the Lake Eyre Basin is one of the less developed basins (1 dam storing 14 GL). We compared the long-term responses of waterbird communities in the two river basins at river basin, catchment and major wetland scales. Waterbird abundances were strongly related to river flows and rainfall. For the developed Murray–Darling Basin, we identified significant long-term declines in total abundances, functional response groups (e.g., piscivores) and individual species of waterbird (n = 50), associated with reductions in cumulative annual flow. These trends indicated ecosystem level changes. Contrastingly, we found no evidence of waterbird declines in the undeveloped Lake Eyre Basin. We also modelled the effects of the Australian Government buying up water rights and returning these to the riverine environment, at a substantial cost (>3.1 AUD billion) which were projected to partly (18% improvement) restore waterbird abundances, but projected climate change effects could reduce these benefits considerably to only a 1% or 4% improvement, with respective annual recovery of environmental flows of 2,800 GL or 3,200 GL. Our unique large temporal and spatial scale analyses demonstrated severe long-term ecological impact of water resource development on prominent freshwater animals, with implications for global management of water resources.

KEYWORDS
biodiversity loss, dams, diversions, freshwater, Lake Eyre Basin, Murray–Darling Basin, regulation, wetlands

1 | INTRODUCTION

The world's biodiversity is experiencing high extinction rates (Pimm & Raven, 2000), particularly in freshwater compared to terrestrial or marine ecosystems (Millennium Ecosystem Assessment, 2005). Habitat loss and degradation, invasive species, overharvesting, pollution and climate change are all damaging freshwater ecosystems (Dudgeon et al., 2006). Water resource developments from building of dams, floodplain developments and abstraction of water have caused widespread degradation of freshwater habitats (Lemly, Kingsford, & Thompson, 2000). This is primarily due to the estimated 16.7 million large dams around the world (>.01 ha, storing 8,070,000 GL) (Lehner et al., 2011), projected to increase in numbers (Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). Despite increasing capacity to measure alterations to flow regimes (Nilsson, Reidy, Dynesius, & Revenga, 2005; Poff & Zimmerman, 2010), their ecological consequences and the pervasiveness of this threat (Vörösmarty et al., 2010), few continuous long-term and spatially extensive biological data sets exist to assess ecological impacts. Most analyses are focused on single wetlands or rivers (Lemly et al., 2000), seldom entire river basins. Water resource developments continue to acutely affect freshwater ecosystems, particularly in dryland regions of the world, given continued competition for scarce water resources, exacerbated by climate change impacts (Barros et al., 2014). There is a pressing need to exemplify such impacts in order to promote sustainable use of global freshwater resources.

Australia has low fresh water availability (~70% <500 mm/year, Stafford Smith & Morton, 1990), reflected in an order of magnitude less annual renewable water resources (336,000 GL/year), compared to other continents, coupled with intense competition for water, with the highest average per capita use globally (2.781 ML p^{-1} yr^{-1} cf. global average of 0.502 ML p^{-1} yr^{-1} (Gleick et al., 2011). Most (~65%) is diverted for irrigated agriculture (State of the Environment Committee, 2011), supplied by dams in the southeast where most agricultural and urban water development occurs (Kingsford, 2000). Of Australia's 12 river basins, most water is diverted from the Murray–Darling Basin (Leblanc, Tweed, Van Dijk, & Timbal, 2012), with the similarly sized Lake Eyre Basin ranking among the least developed (Figure 1, Table 1). These two inland river basins cover about 29% of the continent, with reasonably similar areas of wetlands (Table 1). Lake Eyre Basin flows are highly ephemeral with just less than a third of the mean annual flow of the Murray–Darling Basin, although the Darling River is similar in mean annual run-off to Cooper Creek, the Murray River has considerably more water than the other rivers (Table 1).

Ecological impacts of water resource developments have affected rivers and floodplains of the Murray–Darling Basin (Arthington & Pusey, 2003). This has resulted in formal acknowledgement to the Ramsar Bureau that three Ramsar-listed sites in the Murray–Darling Basin (Lower Lakes, Coorong and Murray Mouth; Macquarie Marshes and Gwydir wetlands) have undergone likely ecological change as a result of human impacts.
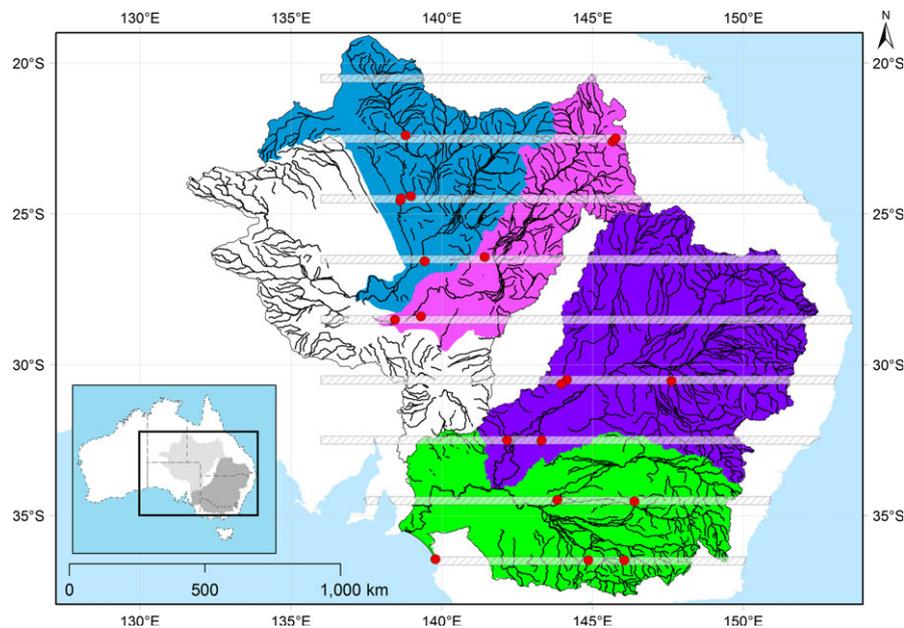

FIGURE 1 Locations of annual aerial surveys (1983–2014) of waterbirds (50 species), across eastern Australia. Surveys were flown each year over up to 900 wetlands, along nine survey bands (30 km wide, hatched bands), across the developed Murray–Darling Basin (dark grey) and undeveloped Lake Eyre Basin (light grey) and their two respective rivers: Georgina-Diamantina Rivers (blue), Cooper Creek (pink), Darling River (purple) and Murray River (green). The five most important wetlands on each river were identified (filled red circles, Lake Katherine [LK], Lake Mumbleberry [MU], Lake Phillippi [LP], Lake Torquinie [LT], Goyders Lagoon [GL], Lake Galilee [LG], Lake Dunn [LD], Lake Yamma Yamma [LY], Lake Hope [LH], Lower Cooper Lakes [CL], Cuttaburra Channels [CC], Macquarie Marshes [MM], Menindee Lakes [ML], Paroo overflow lakes [PO], Tallywalka system [TS], Corop wetlands [CW], Fivbough Swamp [FS], Lake Mokoan [LM], Lowbidgee [LB]).

Subsequently, Australia embarked on one of the world's more ambitious rehabilitation projects, aiming to return water (2,750 GL/yr) to freshwater ecosystems through a reallocation of water diverted to irrigation (>$3.1 billion). This remains highly contentious, primarily because of socio-economic impacts on irrigation communities; poor understanding of social-ecological impacts; little large-scale evidence for widespread ecological impact and; scepticism that returning water to rivers will redress the problem. As elsewhere, the Australian Government relied primarily on a hydrological surrogate (i.e., changes to flow regime) to assess ecological impacts and rehabilitation outcomes (CSIRO, 2008; Mosley, Zammit, & Leyden, 2010). Demonstrated ecological impacts on populations or assemblages of biota are spatially and temporally patchy for different organisms, including waterbird communities (Arthur et al., 2012; Hamdi, Touihri, & Charfi, 2012), a key criterion for Ramsar-listing of wetlands. Waterbirds provide ecosystem services (Green & Elmberg, 2014) and indicate environmental change in wetlands (Tamisier & Boudouresque, 1994).

We quantified trends in abundance and species richness of waterbird communities, prominently featured in national and international policies (e.g., Ramsar Convention), in the developed Murray–Darling Basin and the similarly sized but undeveloped Lake Eyre Basin (Figure 1, Table 1). Both basins have similar areas of wetland but differ considerably in water resource development, including number of large dams, capacity for storage and annual diversions of water (Table 1). We used a long term (32 years) and spatially expansive (29% of continent) annual waterbird survey (Kingsford & Porter, 2009), focused at three spatial scales: basin, river and individual wetlands. We did this by controlling for responses of waterbird populations to variables influencing waterbird communities including flow, hunting, rainfall and Southern Oscillation Index (SOI) (Norman & Chambers, 2010). We then predicted the potential effectiveness of returning varying levels of environmental water on waterbird abundance for the Murray–Darling Basin, as well as incorporating potential effects of climate change.

2 | MATERIALS AND METHODS

2.1 | Aerial surveys of waterbirds

We did aerial surveys of waterbirds, annually (1983–2014) on wetlands within nine survey bands (30 km wide), intersecting the Lake Eyre Basin and Murray–Darling Basin (Figure 1, Table 1, Kingsford & Porter, 2009). We surveyed the same wetlands within the survey bands, representing 13.5% (Murray–Darling) and 10.8% (Lake Eyre Basins). Mean numbers of wetlands surveyed varied with wet and dry periods: 356.3 ± 150.4 SD (range 116–714) in the Murray–Darling and 78.8 ± 41.7 SD (17–208) in the Lake Eyre Basin (Table 1). Waterbirds on all wetlands (>1 ha) were identified and estimated from an aircraft flown at a height of 30–46 m and a speed of 167–204 km/hr, within about 150 m of the shoreline, where waterbirds usually congregate (Kingsford & Porter, 2009). Estimated numbers of each waterbird species, apart from small grebes, egrets, shorebirds and unidentified terns which were grouped (hereafter all called species, Table S1) were recorded on digital audio recorders.

We focused our analyses on three decreasing spatial scales: basin, river (two in each basin) and major wetlands (10 in each basin, Figure 1). Major wetlands usually supported most waterbirds (Kingsford & Porter, 2009). These 10 highest ranked wetlands in the Murray–Darling and Lake Eyre Basins supported an annual average of 60% and 69% of all waterbirds (1983–2014), respectively.

2.2 | Analytical approach

We analysed long-term trends between the developed and undeveloped systems at basin, river and wetland scales, considering effects of environmental drivers. We separately modelled four categories of responses: species' richness, total abundance, abundances of five different functional response groups and abundances of individual species (>5 annual occurrences, 50 species, Table S1). The functional response groups (ducks and grebes, herbivores, large wading birds, piscivores and shorebirds, Table S1, Kingsford & Porter, 1994) allowed partitioning of waterbird populations, reflecting different components or niches of freshwater ecosystems (e.g., fish-eating community), despite overlap in prey. We also examined trends and relationships of explanatory variables for each hunted species (n = 9) separately and as a combined total (Table S1).

Selected explanatory variables were directly or indirectly related to wetland habitats or life history of waterbirds (1982–2014), including flow, local rainfall, year, Southern Oscillation Index (SOI) and Dipole Mode Index (DMI), corresponding to spatial scale of analysis (Table S2). Rainfall and flow variables were included only once in each model, at relevant spatial scales (Tables S2 and S3). Nine waterfowl species (Table S1) are predominantly hunted for recreation or pest mitigation in southeastern Australia, potentially a significant driver of populations. We included two indices of hunting (Table S2) because harvest data for the period were not available: total annual numbers of recreational licensed hunters in eastern Australia (New South Wales, Queensland, South Australia and Victoria) and numbers of ducks shot for pest mitigation, mainly in rice growing areas of New South Wales.

All explanatory variables were derived for the period October to September to explain waterbird community responses in the October survey of the following year. We included additional lagged (1 year) variables for flow and local rainfall, recognizing potential recruitment of waterbirds. For flow at the basin and river scales (1982–2014), we aggregated available annual flows from gauges (Table S3), immediately upstream of where wetlands were distributed (Figure 1), limiting double counting of flows. This was not always possible (e.g., Murray River) where we needed to include potential local and tributary inflows. This caused some inflation of the flow index but captured contributions of distributary systems. At the wetland scale, we used total annual flow (1982–2014) at the closest upstream gauge, reflecting potential habitat loss and degradation, downstream of major diversions. We obtained monthly Southern Oscillation Indices (Bureau of Meteorology, http://www.bom.gov.au/climate/current/soi htm1.shtml), calculating an annual monthly average estimate, given flooding and drying cycles correspond to El Nino and La Nina in

TABLE 1 Wetland areas and degree of water resource development in the developed Murray–Darling and undeveloped Lake Eyre Basins and their constituent rivers. Total wetland areas and levels of water resource development (storage capacity, number of dams, annual average diversions) (see Figure 1), over which surveys of waterbird communities were performed annually (1983–2014)

Scale	Mean annual flow (GL)[a]	Wetland area (km^2)[b]	Dam capacity (GL)	No. of dams	Annual diversions (GL)	No. of wetlands inundated
Murray–Darling Basin	23,850	65,701	29.893	240	6,794 [5,633–7,956][c]	356.25 [116–714][f]
Murray river	14,493	19,125	23,007	173	5,196 [4.037–6,356][c]	171.94 [56–386][f]
Darling river	3,515	46,486	6,886	67	1,598 [1,284–1,912][c]	184.32 [50–383][f]
Lake Eyre Basin	8,638	102,167[e]	14	1	7[d]	78.75 [17–208][f]
Cooper Creek	3,150	38,752	<1	1	7[d]	36.59 [8–90][f]
Georgina-Diamantina rivers	1,300	41,891	0	0	<1[d]	32.47 [8–76][f]

[a]Sources include National Land and Water Audit (2001) for the two basins and CSIRO (2008) for the Murray River (measured at Wentworth) and Darling River (measured at Bourke) and McMahon, Murphy, Peel, Costelloe, and Chiew (2008) for Cooper Creek (measured at Currareva) and Georgina-Diamantina Rivers (measured at Birdsville).

[b]Areas for the Lake Eyre Basin calculated from GeoScience Australia 1:250,000 waterbody layer (Geoscience Australia, 2006), included only Cooper Creek and Georgina-Diamantina Rivers while Murray River and Darling River make up the entire Murray–Darling Basin.

[c]Mean [±95% CI] annual diversions (2003–2012, unpublished data Murray–Darling Basin Authority).

[d]Data source (National Land and Water Audit, 2001).

[e]Includes additional western rivers.

[f]Average (min–max) inundated wetlands surveyed (1983–2014).

Australia (Puckridge, Walker, & Costelloe, 2000). We calculated an annual monthly average estimate from monthly Dipole Mode Index (OOPC, http://stateoftheocean.osmc.noaa.gov/sur/ind/dmi.php), given major flooding and drying in Northern Australia associates with the Indian Ocean Dipole cycles (Ashok, Guan, & Yamagata, 2003). We also used total local annual rainfall near major wetlands (Table S3), important in intermittent filling of wetlands. For rainfall at the river and basin scale, we formed indices which included all the local rainfall estimates, aggregated to the relevant scale (Table S3). We also included rainfall for four regions outside the two basins, assessing possible continental effects of habitat availability (Table S2).

We examined long-term trends in flow and rainfall in the Murray–Darling and Lake Eyre Basins. Long-term records of flows were not available across the basin and so we used gauges on the main rivers: Murray River (Euston and Mildura Gauges, 1913–2014); Darling River (Wilcannia, 1913-2014); Cooper Creek (Currareva and Cullyamurra, 1940–2014) and Diamantina River (Birdsville, 1950–2014). For rainfall at the basin scale, we used gauges across the basins (1913–2014, Table S3). We calculated 5-year standardized (z-score) averages and the cumulative 10-year linear trend for log-transformed ($\ln(x + 1)$) rainfall and flow. We tested for any significant monotonic trends in the log-transformed flow and rainfall, using the Kendall rank correlation within the KENDALL package (Mcleod, 2011) in R language (R Core Team, 2014).

2.3 | Statistical approach

We modelled measures of the waterbird community, in relation to the independent explanatory variables. We used a log-linear model where the slope of year (β) described the linear trend in the log-transformed abundance ($\ln(N_t + 1)$). The log-transformation of

abundance forced linearity on the exponential growth model, stabilizing error variances. The coefficient of year expressed the annual rate of exponential growth or exponential decline, convertible to an annual percentage: $(e^\beta - 1) * 100$. We tested for trends in measures of the waterbird community: species richness, total abundance of waterbirds, abundances of the five functional response groups at basin, river and wetland scales, analysing trends of the 50 waterbird species. Variables were tested for non-normal distribution using the Shapiro-Wilk test, requiring natural logarithm transformation of flow and rainfall. Correlation between annual rainfall and flow volumes in the Murray–Darling basin ($r = .61$) and Lake Eyre basin ($r = .67$) was assumed not to distort model estimation (Dormann et al., 2013). Collinearity decreased at the catchment and wetland scales, given high discrepancy between the source of flows and local rainfall. To deal with model uncertainty for the most appropriate set of explanatory variables from the candidate pool, we used a Bayesian model averaging approach, assessing model uncertainty by examining all possible models (Ghosh & Ghattas, 2015; Hoetting, Madigan, Raftery, & Volinsky, 1999). Model averaging methods perform well in the presence of high levels of collinearity (Freckleton, 2011). We chose a Bayesian model selection approach focusing on our key objective to confirm/falsify the existence of a long-term trend in waterbird abundance, as well as our expectation to correctly identify the existence of a trend, with increasing sample sizes (Aho, Derryberry, & Peterson, 2014) and consistently estimate the underlying process (Casella, Girón, Martínez, & Moreno, 2009; Kass & Raftery, 1995).

We considered the following linear regression (Equation (1)),

$$y = \alpha_\gamma + X_\gamma \cdot \beta_\gamma + \varepsilon_\gamma \quad \varepsilon \sim N(0, \sigma^2 I), \tag{1}$$

where y was the waterbird response measure; α_i a constant; X_γ the subset of all explanatory variables X; β_γ a vector of coefficients; ε the

error term and; γ one model out of 2^K possible models where K represented all potential explanatory variables. Models were then averaged, using the posterior model probability (PMP), implied by Bayes' theorem (Equation (2)),

$$p(M_\gamma|y, X) \propto \frac{p(y|M_\gamma, X) \cdot p(M_\gamma)}{p(y|X)}, \qquad (2)$$

where $p(M_\gamma|y, X)$ denoted the PMP, proportional to the model's marginal likelihood $p(y|M_\gamma, X)$ times the model's prior probability $p(M_i)$. Renormalizations leads to the PMPs and the model weighted posterior distribution for the statistic θ. Thus, the β-coefficients were given by (Equation (3)):

$$p(\theta|y, X) = \sum_{\gamma=1}^{2^K} p(\theta|M_\gamma, y, X) \cdot p(M_\gamma|X, y). \qquad (3)$$

We elicited the priors on parameters and models as follows. As both α_γ and σ^2 were common to all models, we used uniform priors, reflecting our lack of knowledge: $p(\alpha_\gamma) \propto 1, p(\sigma^2) \propto \frac{1}{\sigma^2}$. For the parameters β_γ, we formulated beliefs on coefficients into a normal distribution with a specified mean of zero (reflecting poor knowledge) and a variance structure according to the robust Zellner's g prior (Liang, Paulo, Molina, Clyde, & Berger, 2008), (Equation (4)):

$$\beta_\gamma|g \sim N\left(0, \sigma^2\left(\frac{1}{g}X'_\gamma X_\gamma\right)^{-1}\right). \qquad (4)$$

We used a common approach of the unit information prior (UIP) to set $g = N$ for all models (Kass & Wasserman, 1995), attributing the same information to the prior as within one observation. To avoid overfitting and maintain model complexity at a reasonable size for our sample size ($n = 32$), we set a binomial-beta hyper-prior on the a priori inclusion probability of any model and corresponding hyper-prior value of the model size of three. A value of three defined the prior expected value of the model, rather than an absolute limit. Thus, model size was not limited to three explanatory variables.

Our certainty for an explanatory variable was estimated as the probability that the variable was included in considered regression models (Liu & Motoda, 2007). This measure was referred to as the posterior inclusion probability (PIP), estimated by (Equation (5)):

$$\text{PIP} = p(\beta_\gamma \neq 0|y) = \sum\nolimits_{\beta_\gamma \neq 0} p(M_\gamma|y, X) \qquad (5)$$

As we compared many possible models (2^{27}), we employed the Markov Chain Monte Carlo Model Comparison (MC^3) method (Madigan, York, & Allard, 1995) to focus on model regions with high posterior model probabilities, approximating the exact posterior probability efficiently. To obtain posterior distributions and means of our parameters, we used 100,000 draws from the MC^3 sampler, following 100,000 burn-in draws. Changes in waterbird responses were estimated by incorporating a yearly trend covariate ($\beta_{2,\gamma}$), within the model averaging process (Equation (6)):

$$y = \alpha_\gamma + \beta_{1,\gamma} \cdot X_\gamma + \beta_{2,\gamma} \cdot \text{Year}_\gamma + \varepsilon_\gamma \ \varepsilon \sim N(0, \sigma^2 I). \qquad (6)$$

All computations were performed in the R environment (R Core Team, 2014) using the BMS package (Zeugner & Feldkircher, 2009). As a measure of goodness of fit, we calculated Efron's pseudo R^2 (squared correlation between the predicted abundances and actual abundances; Efron, 1978). Predicted abundances were derived from model averaged coefficient estimates.

2.4 | Flow restoration in the Murray–Darling Basin

We tested the potential benefits of flow restoration for waterbird abundance in the Murray–Darling Basin, examining relationships between explanatory variables and total waterbird abundance. We predicted waterbird responses to five flow scenarios for major policy decisions: without water resource development, baseline (without the Murray–Darling Plan restoration, status quo in June 2009), two rehabilitation scenarios of increasing environmental flows by 2,800 GL each year (2,750 GL was the final position following a 50 GL reduction but never modelled) and 3,200 GL each year, and the current effects (i.e., 1°C increase) of climate change on the baseline model, with a 2030 Medium modelled Climate (Chiew et al., 2010). A flow scenario, incorporating rehabilitation and climate change did not exist, given the complexity of predicting changes in water use across different sectors.

For each scenario, we used flow models developed by the Murray–Darling Basin Authority at all river gauges for the period, 1902–2008 (Mosley et al., 2010), with annual flow data from the main flow gauges on major rivers (Table S3). The flow gauges were immediately upstream of the major wetlands, the primary waterbird habitats. These included seven flow gauges in the Darling River and eight flow gauges in the Murray River (Table S3). We also incorporated historic SOI values and rainfall records across the Murray–Darling Basin, Lake Eyre Basin and outside these regions, including 1-year lags (Table S2). We then used posterior average coefficients to predict total waterbird abundances, under the four different flow scenarios, comparing the effects of flow restoration on waterbird populations across the Murray–Darling Basin, compared to the baseline, including the impacts of climate change projection on the baseline scenario.

3 | RESULTS

3.1 | Flow and rainfall

The developed Murray–Darling Basin and undeveloped Lake Eyre Basin experienced similar highly variable dry and wet periods over about a century (Figure 2). Average annual rainfall indices (and coefficients of variation) (1900–2014) were, respectively, 422 mm (24%) and 285 mm (43%). Both river basins experienced a long dry period from the early 1920s until the 1950s, followed by short dry periods in the mid 1960s and 1980s and a long dry period in the mid 2000s
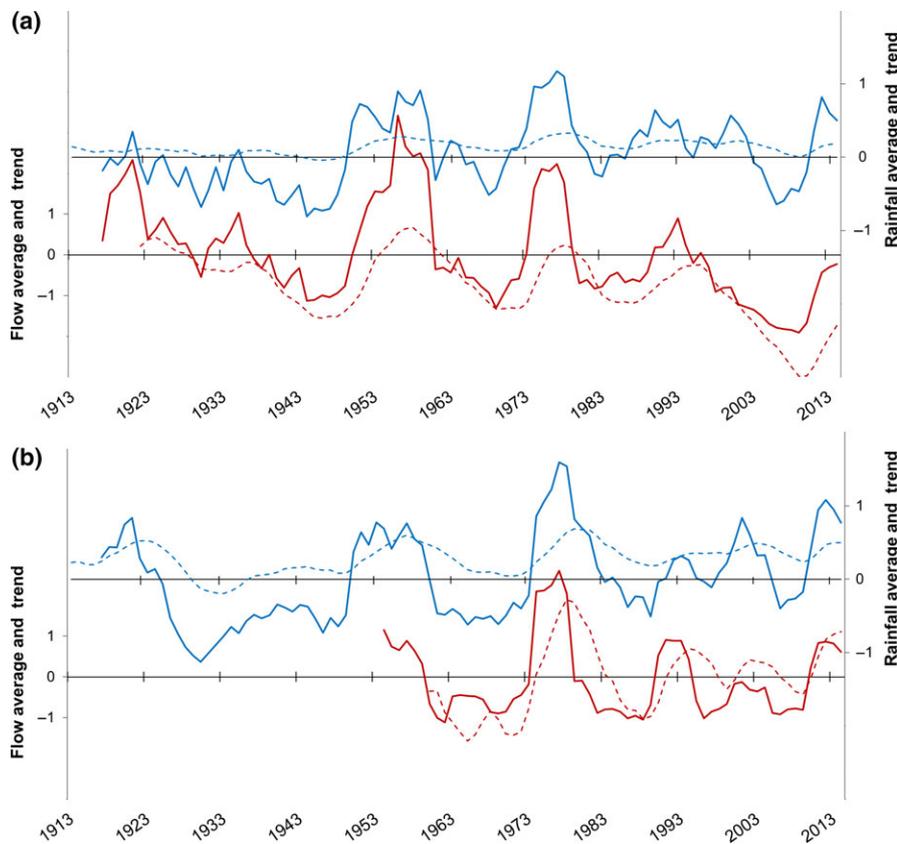
(a)

(b)

FIGURE 2 Annual averages and trends in rainfall (blue) and flows (red) in the developed Murray–Darling Basin and the undeveloped Lake Eyre Basin, 1913–2014. Long-term 5-year moving annual averages of standardized (z-score) rainfall and river flows (continuous lines) and their cumulative, 10-year annual trend (adding these 5 year averages; dashed lines) for (a) the developed Murray–Darling Basin and (b) the undeveloped Lake Eyre Basin.

(Figure 2). There were also matching high rainfall peaks in the 1950s, 1970s, early 2000s and about 2010–2012 (Figure 2). There was no trend in annual rainfall in the developed Murray–Darling Basin (tau = .098, n = 115, p = .121, Figure 2a) and a slightly positive trend in the undeveloped Lake Eyre Basin (tau = .126, p = .045, n = 115, Figure 2b). There were no trends in annual rainfall for three river scales, the Darling River (tau = .092, n = 115, p = .144), the Murray River (tau = .061, n = 115, p = .331) and Cooper Creek (tau = .046, n = 115, p = .462) but an increase in the Georgina-Diamantina Rivers (tau = .247, n = 115, p < .001).

Dry and wet rainfall periods were reflected in flow peaks and troughs in the two river basins (Figure 2). Mean and variability (coefficient of variation in parentheses) of annual flows differed between the river basins, reflecting differences in quantity and variability of rainfall: 1,157 GL for Murray–Darling Basin (54%) and 743 GL for the Lake Eyre Basin (129%). Contrastingly, there was a long-term significant decline in flows in the developed Murray–Darling Basin (1913–2014, tau = −.208, n = 102, p = .002, Figure 2a), compared to no trend in the undeveloped Lake Eyre Basin (1950–2014, tau = −.011, n = 65, p = .905, Figure 2b), consistent with levels of water resource development (Table 1). There was also a long-term significant decline in flows in the Murray River (1913–2014, tau = −.239, n = 102, p < .001), where most diversions occur, but not in the Darling River (1913–2014, tau = −.054, n = 102, p = .422) or Lake Eyre Basin rivers (Cooper Creek: 1940–2014, tau = −.008, n = 65, p = .923; Georgina-Diamantina: 1950–2014, tau = .043, n = 65, p = .614).

3.2 | Waterbird communities

Waterbird abundances were highly variable over the 32-year period in both river basins, with high coefficients of variation for the Murray–Darling (90%) and Lake Eyre Basin (109%), (Fig. S1). On average, waterbird abundances were about one and a half times higher in the Murray–Darling Basin compared to the Lake Eyre Basin and slightly more species (Table S4).

Candidate models of abundance of all waterbirds in the Murray–Darling Basin included a mean of 2.6 significant predictor variables, with reasonable model fit (Table S5). Year had the highest probability of inclusion with a negative relationship followed by Murray–Darling flows with a positive relationship. The remaining 17 variables had considerably lower probabilities of inclusion (PIP < 0.10), indicating low influence on waterbird abundance (Table S5). This was similar for Darling River and Murray River (Table S5).

We used our model of total abundance of waterbirds in the Murray–Darling Basin (Table S5), assuming no year effect, to estimate potential effects of restoring flows to the Murray–Darling Basin (Fig. S2). There were predicted differences in waterbird abundances, among the four flow scenarios, representing different levels of environmental flow and climate change (Fig. S2). An increase of 3,200 GL each year, on the baseline model, increased the numbers of waterbirds by 21% while the 2,800 GL increase in annual flows increased waterbird numbers by 18%. However, this increase was estimated to be reduced by projected climate change, decreasing numbers by about 14%, below the baseline model estimates
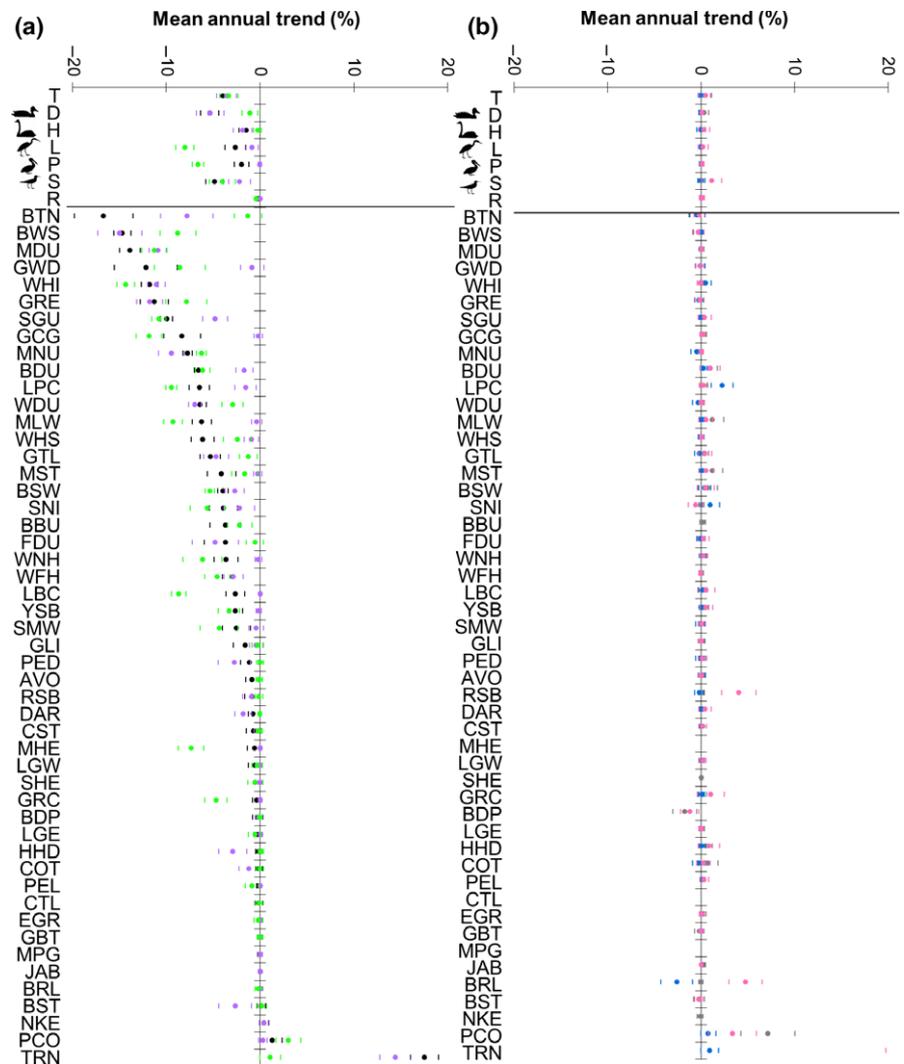
FIGURE 3 Trends in waterbird abundances in the developed Murray–Darling Basin and the undeveloped Lake Eyre Basin and their rivers. Mean (±95% confidence limits) annual trends (1983–2014), relative to average abundance for different waterbird response measures including (a) the developed Murray–Darling Basin (dark grey) and its two rivers (purple-Darling, green-Murray) and (b) the undeveloped Lake Eyre Basin (light grey) and its two rivers (blue—Georgina-Diamantina, pink-Cooper). Horizontal lines separate grouped waterbird measures (T-total, D-ducks, H-herbivores, L-large waders, P-piscivores, S-shorebirds, R-species' richness) from individual species (ranked trends, see Table S1 for acronyms matching species' names and trends [Table S7]) .

(Fig. S2). If this relationship remained for the climate change scenario and environmental flows, we estimated that there would be about a net 1% and 4% increase in waterbird numbers with 2,800 GL and 3,200 GL of environmental flows, respectively, and projected climate change, based on the relationships between flow and waterbird abundances, using the period of record (1900–2008).

Candidate models explaining waterbird abundance in the Lake Eyre Basin included an average of 3.2 predictor variables, with reasonably good fit (Table S5). Eleven variables had probabilities above chosen threshold of 0.1 (PIP) for inclusion (Table S5). Annual rainfall in the Lake Eyre Basin had the highest PIP (positive) followed by 1-year lag of hunting (negative) and 1-year lag of annual rainfall in south eastern Australia (positive). Generally, flow and rainfall within the Lake Eyre Basin and Year had positive relationships with waterbird abundance at different spatial scales, with rainfall in the east and south and hunting negatively associated with abundance of waterbirds (Table S5). This was similar for the two rivers (Table S5).

We separately modelled the relationships between predictor variables, including hunting, on total numbers of all hunted species of ducks counted and counts of each of the nine hunted species (Table S6). There was generally a weak association with hunting,

with a probability of inclusion of less than 10%, for all hunted species and each species individually (Table S6). Most candidate models were dominated by the same predictor variables affecting total abundances of waterbirds at the different spatial scales. The highest probability of inclusion for negative effect of hunting was for Australian wood duck, hardhead, Australasian shoveler, plumed whistling-duck and all hunted species (Table S6). Strongest effects were usually negative and operating a year after hunting.

In the Murray–Darling Basin, waterbird abundances declined significantly: an average 3.99% annual decline or a 72% decline over the 32-year period (Figure 3a, Fig. S1, Table S4), with substantial decreases in abundances between the first and last decades (58–76%, Table S4). All functional response groups of waterbirds and 60% of species declined (Figure 3a, Fig. S1c,d, Table S4). Declines were more severe in the Murray River than in Darling River (Figure 3a, Table S4).

These patterns were also reflected in significant declines across species in the developed Murray–Darling Basin and its two catchments (Figure 3). Abundances of 56% of the 50 species significantly declined in the regulated Murray–Darling Basin, with more pronounced trends in the Murray River catchment (54% of species),
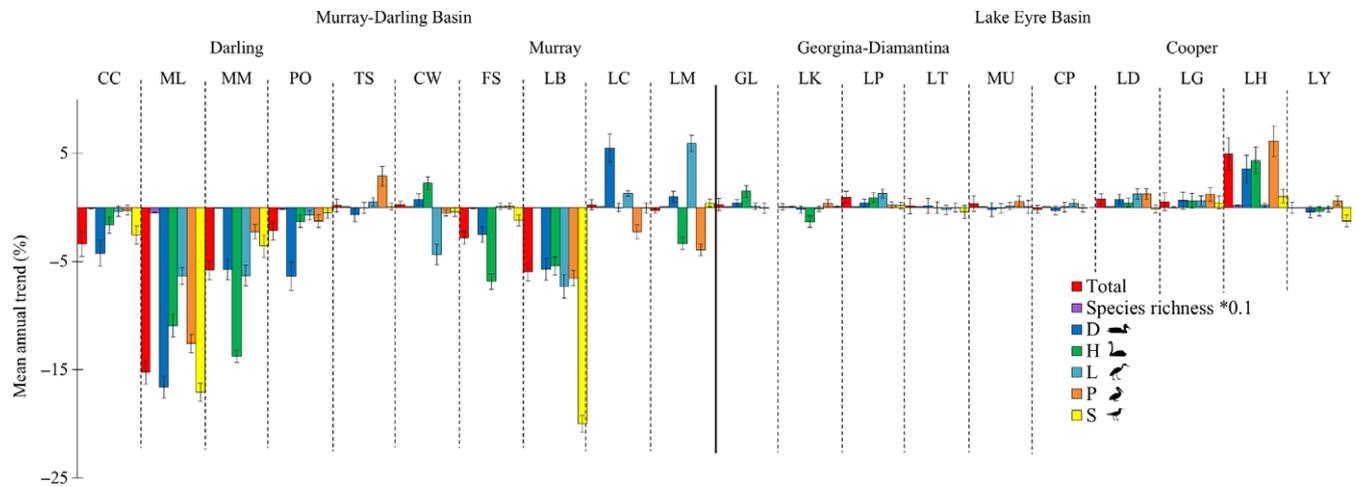
FIGURE 4 Trends in waterbird abundances in five major wetlands in each of two rivers in the developed Murray–Darling Basin and the undeveloped Lake Eyre Basin. Mean (±95% confidence limits) annual trends (1983–2014), relative to average abundance, for seven waterbird response measures (T-total abundance, R-species richness *0.1, D-ducks, H-herbivores, L-large waders, P-piscivores, S-shorebirds) for five major wetlands in the two main rivers of the Murray–Darling Basin (Darling, Murray) and Lake Eyre Basin (Georgina-Diamantina, Cooper). See Table S4 and Figure 1 for letters matching names of wetlands in the rivers and basins.

compared to the Darling River catchment (32% of species) (Figure 3). Abundances of 12 species (24% of species) declined at the basin scale and the two rivers. Only terns (unidentified, Table S1) increased in number at the scale of the Murray–Darling Basin and in the Darling River catchment while only pied cormorants increased in the Murray River catchment (Figure 3). In the Lake Eyre Basin and its two catchments, only abundances of brolgas (BRL) declined in the Georgina-Diamantina catchment with nine other species increasing at basin or river scale (Figure 3).

Total abundance and that of the five functional response groups also generally declined at the wetland scale in the Murray–Darling Basin (Figure 4). Duck and piscivore functional response groups declined across six of the 10 wetlands while shorebirds declined across five of the 10 wetlands, with only a few functional response groups increasing (Figure 4). The ducks and piscivore functional response groups declined across six of the ten wetlands while shorebirds declined across five of the ten wetlands in the Murray–Darling Basin. Contrastingly, there were few negative trends in abundances of waterbirds in wetlands of the Lake Eyre Basin (Figure 4, Table S4). Few functional groups increased in the Murray–Darling Basin wetlands while only shorebirds declined on two wetlands and all other metrics increased on wetlands in the Lake Eyre Basin (Figure 4).

4 | DISCUSSION

Humans are developing the world's freshwater resources, predominantly by building dams, to meet water demands for drinking, agriculture, industry and hydroelectricity generation. The world's current 6,862 large dams (Lehner et al., 2011) are projected to double by 2030 (Zarfl et al., 2015), exacerbating ongoing degradation of freshwater ecosystems and their services (Lemly et al., 2000). Despite the

landmark report by the World Commission on Dams in 2000 identifying the significant ecological impacts and the need for appropriate environmental assessment (World Commission on Dams, 2000), understanding of large-scale ecological changes caused by water resource developments remains relatively poor, compared to hydrological changes to flow regimes (Grill et al., 2015; Nilsson et al., 2005). Without good understanding and examples of these ecological impacts and also rehabilitation efforts, communities and their governments may not invest sufficiently in rehabilitation of large freshwater ecosystems or avoid serious impacts.

We have provided strong evidence of the ecological consequences of large-scale impacts of water resource development. There were consistent and strong declines in waterbird abundances over 32 years at three spatial scales, the basin, river and wetland in the developed Murray–Darling Basin, where cumulative annual flow decreased because of water resource development, with its 240 large dams and average annual diversions of about 6,800 GL (Table 1). Abundances in the Murray–Darling Basin declined by 72% over 32 years, compared to no significant changes in the nearby undeveloped and similarly sized Lake Eyre Basin (Figure 2, Table 1). This is reinforced by our identification of flow as the main driver of waterbird abundances. The negative trends were consistent across five functional response groups and most species of waterbirds, representing different niches of freshwater ecosystems, indicative of widespread ecosystem decline. This contrasted with a general absence of trends in the adjacent undeveloped Lake Eyre Basin where there was no trend in flow volumes.

This indicated widespread ecosystem decline in the Murray–Darling Basin, as waterbird distribution and abundance is primarily dependent on prey availability. Waterbird species are top-level predators, feeding on fish, frogs, invertebrates and vegetation. They occupy a wide range of niches in a wetland, equipped with different morphological, behavioural and physiological adaptations (Kingsford

& Norman, 2002; Paracuellos, 2006). Consistent declines across all functional response groups and many species reflected growing evidence of declines in waterbird numbers and breeding (Leslie, 2001; Paton, Rogers, Hill, Bailey, & Ziembicki, 2009; Ravenscroft & Beardall, 2003; Reid, Colloff, Arthur, & Mcginness, 2013), but also their food and nesting resources including invertebrates, fish and vegetation across the Murray–Darling Basin. This probably also explained the difference in wetland areas between the two river basins (Table 1), given that almost half of the wetlands in the Murray–Darling Basin may have been lost (Kingsford, Brandis, et al., 2004).

The strong positive relationship between flows and waterbird communities is grounded on creation and maintenance of habitat for feeding and breeding (Roshier, Robertson, Kingsford, & Green, 2001). Large floodplain wetland systems lie at the end of rivers, providing considerable resources for organisms in the food web (Ward, 1998). These habitats are among the most globally threatened freshwater environments (Scheffer et al., 2015; Tockner & Stanford, 2002). Our analyses were necessarily correlative, given water resource development is a widespread ramp disturbance (Lake, 2000), progressive over more than a century across the Murray–Darling Basin (Leblanc et al., 2012). However, there is good evidence that declines in waterbird communities were primarily driven by diversions of water upstream by controlling dams. First, our modelling consistently showed positive relationships between flows and waterbird communities, not only in the Murray–Darling Basin but also in the Lake Eyre Basin and their catchments (Table S5). Second, declines in waterbird communities were consistent across spatial scales in the developed Murray–Darling Basin, contrasting with the absence of declines in the undeveloped Lake Eyre Basin, at all spatial scales. In the Murray–Darling Basin and its catchments, declines in waterbird communities coincided with reductions in river flows, despite no changes in rainfall (Figure 2). Flow reduction in the Murray–Darling Basin is clearly established (Leblanc et al., 2012), a pattern not repeated for the Lake Eyre Basin and its catchments. The Murray River catchment showed more severe declines than the Darling River catchment, possibly reflecting differences in lags in water resource development which occurred later in the Darling River catchment, compared to the Murray River catchment. Also, the flow modelling was likely to be relatively insensitive to major reductions in floodplain inundation, shown when the hydrological modelling used to underpin our analyses was compared to a stochastic statistical model (Ren & Kingsford, 2011). Further, there is widespread alienation of floodplain areas by levee banks in the Darling River catchment (e.g., Macquarie Marshes, Steinfeld & Kingsford, 2013), coupled with water resource development, contributing to declining habitats for waterbirds. These factors probably contributed to the larger declines in waterbird abundances in the Darling River, compared to the Murray River.

Most major rivers in the Murray–Darling Basin have experienced reductions of 40% or more in flows reaching their floodplain wetlands (Leblanc et al., 2012), coinciding with declines in waterbird communities on most of the key wetlands in the Murray–Darling Basin (Figure 4). Consistent with this argument, the Paroo River overflow lakes in the Murray–Darling Basin supplied by the Paroo River (Figure 1), with no water resource development, experienced low declines compared to most other wetlands in the Murray–Darling Basin (Figure 4). No such trends for flow existed in the Lake Eyre Basin, with some evidence of a slight increase (Figure 2, Table S4). Other factors may also be contribute to long-term decline including pollution (e.g., salinization, acidification) (Kingsford et al., 2011), changes to invertebrate communities (Jenkins & Boulton, 2007) and vegetation communities (Bino, Sisson, Kingsford, Thomas, & Bowen, 2015; Thomson et al., 2012) which provide nesting habitats and primary production to wetlands. Many of these changes are also influenced by water resource developments. There are also potential impacts of invasive species on wetlands and rivers (e.g., European carp *Cyprinus carpio* (Koehn, 2004)), which may be confounding the main drivers although invasive species occur in the rivers of the Lake Eyre Basin. There may also be subtle interactions between basins and wetlands within basins affecting waterbird abundances.

Abundances of hunted waterfowl, among the more numerous species surveyed, were weakly negatively related, usually lagged by a year, to hunting in most models, indicative of the potential impact of breeding adults affecting subsequent recruitment of individuals (Table S6). This should be a consideration in declaration for hunting seasons when there is little recruitment, such as in dry years (Kingsford, 1989), as this may further drive declines in hunted species. Importantly, hunting was not as strong a driver as flow and rainfall. Water resource development represented a more significant driver of declines in abundances of hunted species of waterfowl, than hunting.

With a strong relationship between river flows and waterbird ecology, there are opportunities to address degradation of aquatic ecosystems through rehabilitation and restoration of flow regimes. Our analyses indicated that the Australian Government's return of 2,750 GL each year of environmental flows to the rivers of the Murray–Darling Basin would return about 18% of the waterbird abundances, compared to the baseline of development before rehabilitation. However, when we incorporated the projected effects of climate change to the baseline model, there was a considerable reduction of 14% in numbers, below our baseline estimates (Fig. S2). This indicated that the environmental flow restoration would still have a positive effect on waterbird numbers but it may only increase numbers by 1%–4%, given the projected effects of climate change and assuming that the relationship found for the baseline model was maintained for future climate change. Unfortunately, there was no flow scenario that combined the effects of climate change and restoration.

Freshwater resource development of the world's rivers continues unabated, primarily through the building of dams to divert water (Zarfl et al., 2015) exacerbating ongoing degradation of wetlands and their services (Lemly et al., 2000). These dams compare poorly to natural wetlands in providing waterbird habitats (Sebastián-González & Green, 2016). We demonstrated widespread degradation, reflected in changes across waterbird communities over three decades.

Waterbirds are a good surrogate for ecosystem health (Green & Elmberg, 2014; Kingsford, Jenkins, & Porter, 2004), given the range of species and niches occupied. There is a need for improved collection and analyses of long-term datasets of biota, including waterbirds, so that governments and local communities can make more informed decisions about the short- and long-term impacts to freshwater ecosystems and their services as well as report on rehabilitation success and failure. Floodplain habitats are among the most globally threatened freshwater environments (Tockner & Stanford, 2002), requiring adequate protection through improved environmental assessments, mitigation of impacts, protected areas, environmental flows and rehabilitation. Our study has major implications for the effects of projected dam building in other parts of the world, including southeast Asia, Africa and South America. The downstream impacts, indicated by large-scale declines of waterbirds, representing most parts of the ecosystem is inevitable once the flooding is reduced, not only impacting destructively on biodiversity but also many ecosystem services provided by rivers and floodplains.

CONFLICT OF INTEREST

None of the authors has any conflicts of interest in relation to this work.

DATA AVAILABILITY

The data are archived in a publicly available database, the National Waterbird survey database https://aws.ecosystem.unsw.edu.au/.

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