

Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands

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Summary

1. River regulation and exotic plant invasion threaten riverine ecosystems, and the two often co-occur. By altering water regimes, flow regulation can facilitate plant invasion by providing conditions that directly benefit invading species, or by reducing competition from native species unsuited to the modified conditions. Integrating water and weed management has the potential to limit riparian plant invasion and maximize the ecological benefit of environmental flows.
2. We surveyed plant communities and modelled flood histories of 24 riparian wetlands along the regulated River Murray, south-eastern Australia. There were no suitable control rivers, so we compared modelled pre- and post-regulation hydrological data to quantify hydrological change in the study wetlands. Regression analyses revealed relationships between hydrological modification and cover of native non-weed, native weed and exotic weed groups and 10 individual species.
3. Exotic cover was highest and native non-weed cover lowest in wetlands that had experienced the greatest change in hydrology – a reduction in peak flow. Native weeds did not respond to hydrological modification indicating that exotic species' success was not reliant on their generalist characteristics.
4. By altering habitat filters, hydrological modification caused a decline in amphibious native non-weed species cover and simultaneously provided drier conditions that directly favoured the exotic species group dominated by terrestrial species. Exotic species were potentially further assisted by human-mediated dispersal.
5. Species and functional diversity was inversely related to exotic cover. By shifting the balance between native and exotic taxa and changing community functional composition, flow regulation may disrupt the ecological function and ecosystem services of floodplain wetlands.
6. *Synthesis and applications.* Worldwide, flow regulation has led to riverine ecosystems becoming more terrestrial. The success of most introduced plants relies on minimal inundation. In this study, flood magnitude was more important than frequency, timing, or duration for wetland flora because it reflects spatial extent and depth of flooding. Augmenting natural spring floods with environmental flows will kill terrestrial weeds and facilitate native macrophyte growth. Combined with strategies for managing particular amphibious weeds, we recommend flows of 117 000–147 000 ML day⁻¹ for at least 2 days every 10 years for River Murray wetland weed management.

Key-words: biotic resistance, community assembly, diversity, environmental filters, environmental water, functional composition, habitat generalists-specialists, human impacts, propagule pressure, River Murray

Introduction

Ecological theory suggests that the assembly of biological communities is determined, in part, by environmental conditions that function as a series of environmental sieves, or filters

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(MacArthur & Levins 1967; Diamond 1975; Weiher & Keddy 1995). If a species lacks traits required to occupy the environmental conditions of a habitat, it will be filtered out. Changes to environmental filters will alter the type of organisms that can inhabit an ecosystem, providing opportunities for exotic species to invade, especially if the regional native species pool lacks sufficient diversity (Moles, Gruber & Bonser 2008). By modifying environmental conditions through climate change, eutrophication and river regulation, for example, human actions can indirectly alter the structure and function of biological communities and may facilitate species invasion.

We hypothesize that the abundance of exotic species may increase as a result of environmental modification in two ways. First, if native species are ‘habitat specialists’ adapted to historical conditions, they may be unable to tolerate modified environmental conditions (Evangelista *et al.* 2008). The resultant decline in habitat-specialist native plant populations will benefit invading species that are ‘habitat generalists’ able to occupy a range of conditions, as was the case with invasion of crayfish *Orconectes neglectus chaenodactylus* Williams in Spring River drainage, USA (Larson *et al.* 2009). Cover of native generalists will track exotic cover and increase as well (Fig. 1a). Secondly, if exotic species are pre-adapted (or adapt rapidly: Henry *et al.* 2010) to the modified conditions, they may be able to out-compete both types of native species (Fig. 1b). While abundance of exotic ‘habitat specialists’ would only increase under certain environmental conditions (Fig. 1b), we predict that abundance of exotic ‘habitat generalists’ would increase with any type of environmental change provided the change was to the detriment of a portion of native species (Fig. 1a). Invasion success will be greatest when a decline in cover of native specialists is coupled with environmental conditions that favour exotic specialists.

In this study, we examined whether changes in hydrological conditions caused by river regulation prompted a change in the composition of plant communities and facilitated exotic invasion in floodplain wetlands of the River Murray, Australia. Many riparian plant species have specific ecophysiological

requirements of hydrology (Merritt *et al.* 2010), so changes in flow magnitude, duration, timing, frequency and predictability may alter plant community composition (Arthington *et al.* 2006; Stromberg *et al.* 2007). We tested our two hypotheses (Fig. 1) by examining proportional cover of terrestrial and amphibious native non-weeds, native weeds and exotic weeds. These trends indicated whether hydrological modification altered habitat filters, or if other factors were at play. Comparing the responses of exotic species with native weeds (species native to Australia but invasive elsewhere) helps to determine whether exotic weeds increased primarily because they are habitat generalists with general ‘weedy’ traits (van Kleunen, Weber & Fischer 2010), or whether they have specific advantages associated with the type of hydrological modification experienced, or their close relationship with humans and distinct evolutionary histories (Catford, Jansson & Nilsson 2009).

In a novel approach, we used proportional change from modelled pre- to post-regulation conditions to indicate the extent and direction of change from historical conditions in 24 floodplain wetlands. In this study we specifically focused on alteration of the water regime, which is thought to be the most important disturbance agent in freshwater ecosystems (Raulings *et al.* 2010). We examined specific effects of eight hydrological change variables on eight groups of species and 10 individual species to determine whether some aspects of hydrological change are more influential than others. However, because the flood regime is multivariate, we predict that flora will respond more strongly to the combined change in variables rather than single changes. We show that differences in the composition of exotic and native species pools, and a shift in their proportional cover, can affect the functional diversity of these wetland plant communities. If there is a causal link between river regulation and exotic invasion, hydrological management that targets particular aspects of the flow regime could be used to control riparian exotic weed populations (Howell & Benson 2000; Buckley 2008), which are particularly difficult to manage (Wadsworth *et al.* 2000).

Materials and methods

STUDY REGION AND STUDY SITES

Research was conducted in 24 River Murray wetlands between Hume Dam at Albury and Barmah, south-eastern Australia (see map in Fig. S1, Supporting Information). Of four spatial scales examined in a previous study (Reaches spanning 74 km, Clumps of three wetlands within 2 km of each other, Wetlands, Wetland sections: Catford & Downes 2010), variation in plant community structure mostly occurred at the scale of individual wetlands, thus suggesting that factors critically affecting wetland plants act at this scale. The study wetlands were spread along a contiguous 395 km long stretch of river channel. The upstream end of the stretch was just downstream of a major dam (Hume Dam). Midway along the stretch a largely unregulated tributary (Ovens River) entered, and a major structure (Yarrowonga Weir) diverted water from the River Murray.

Regulation of the River Murray has reduced winter and spring flows and increased summer and autumn flows in the study region (Maheshwari, Walker & McMahon 1995). Irrigation uses 90–98% of

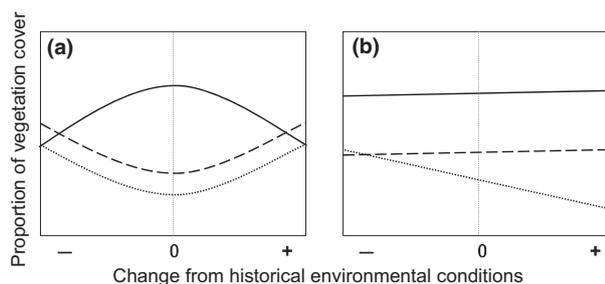


Fig. 1. Two hypotheses to explain the increase in exotic plant invasion under altered environmental conditions: (a) Proportional cover of exotic weeds increases (dotted line), regardless of the direction of environmental change, as a result of a decline in native non-weed cover (solid line). Native weed cover (dashed line) is also predicted to increase in this scenario. (b) Exotic weed cover increases under a change to certain environmental conditions (e.g. shorter flood duration) and is independent of native non-weed and native weed cover, which are largely unaffected by environmental modification.

the diverted water (MDBMC 1995). We analysed flood frequency for 109 years of modelled natural and current daily flows from 1891 to 2000 for gauges at Corowa (upstream of Yarrawonga Weir) and Tocumwal (downstream of Yarrawonga Weir; combined partial duration and annual maximum series, fitted to Generalized Pareto distribution). Small unseasonal floods increased downstream of Yarrawonga, which is related to the way in which water is delivered for irrigation. Large infrequent floods (>40 to 50 years average return interval, ARI) were not altered by regulation. Events that were 2 years ARI in the natural series were 5 years ARI in the current series. Events of 20 year ARI in the natural series were 32 years ARI in the current series. The 24 study wetlands varied in degree of hydrological modification because of variation in downstream location and elevation on the floodplain. Not all hydrological changes were associated with position along the river, but some were.

WETLAND FLOOD REGIME MODELLING

Changes to wetland flood regimes from river regulation were estimated using daily time-step wetland water balance models generated in Microsoft Office Excel (2003) under pre- and post-regulation conditions (Fig. 2). Both models used simulated daily river flow data (source: River Murray Water; MDBMC 2002). Only the 10 years immediately preceding field sampling were considered, as the more distant hydrological history would have had much less influence on determining current vegetation patterns of short-lived, herbaceous species. Over the 10-year modelling period (1 February 1996–31 January

2006), the simulated post-regulation river water level data had a median divergence of 10% (0.22 m) from stage heights measured at the river. For the water balance model, the starting wetland water level was set as the mean wetland depth, and the model commenced on 1 February 1991 to allow 5 years for model convergence.

The water balance of a floodplain wetland is the net result of several gains and losses, calculated over a selected time-step (Poiani & Johnson 1993). The water balance models were based on river water levels relative to wetland commence-to-flow (CTF, the river level when the river and wetland are hydraulically connected) thresholds, evapotranspiration, precipitation and wetland depths. We avoided wetlands where water was extracted or diverted, and those that received agricultural drainage. Local runoff would have been minimal because of the low relief and small size of the wetland catchments. There was no data available for surface-groundwater exchange, but the high fraction of clay in the study wetlands suggests that groundwater recharge or discharge would have been marginal. We assumed an unconstrained hydraulic linkage between river and wetlands such that when the river levels exceeded wetlands' CTF thresholds, the wetland water levels followed river levels. See Appendix S1 (Supporting Information) for details and evaluation of the water balance models.

HYDROLOGICAL MODIFICATION

Using the modelled daily water levels, flood depth, duration and variability, river-wetland connection events, and the timing of flooding

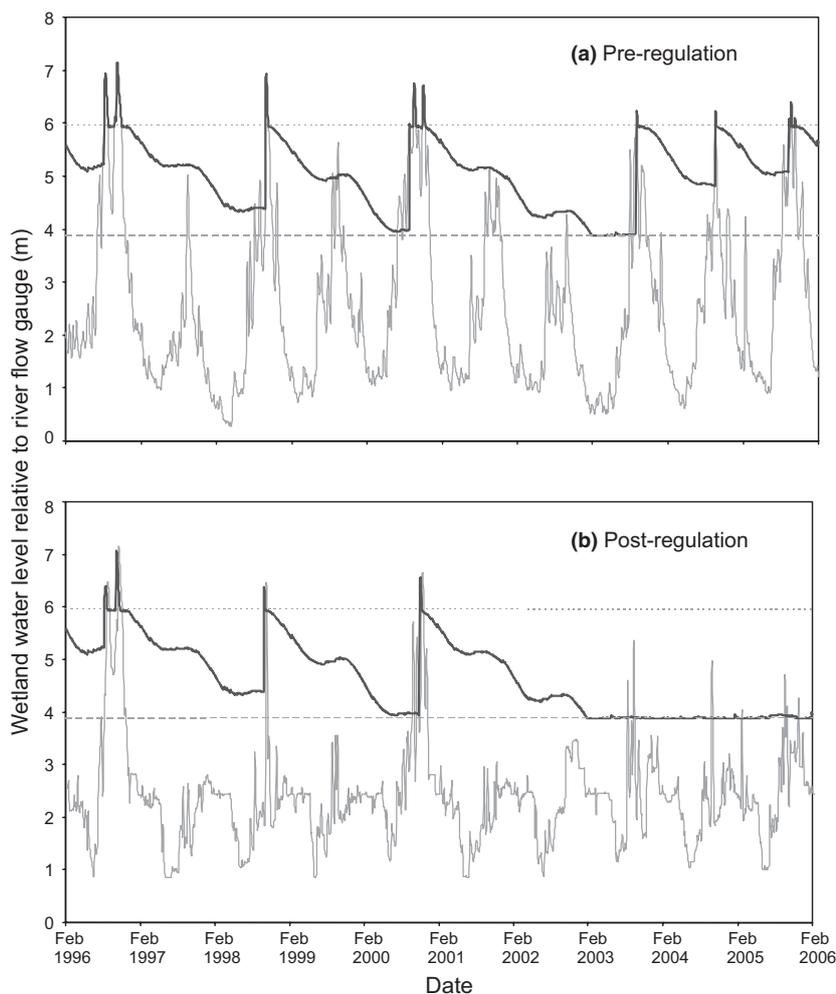


Fig. 2. Modelled daily water levels from 1 February 1996 to 1 February 2006 for an example wetland under (a) pre-regulation and (b) post-regulation conditions. Solid black line, wetland water level relative to river gauge; solid grey line, river water level at gauge; upper dashed grey line, wetland sill level relative to gauge; lower dashed grey line, wetland bed level (lowest point in wetland) relative to gauge. See Table S3 (Supporting Information) for details.

Table 1. Description of eight environmental variables and 18 floristic response variables used in analyses

Variables	Abbreviation
<i>Explanatory variables</i>	
Maximum depth at lowest elevation [m]	Depth max.
Standard error of mean depth at lowest elevation [m]	Depth SE
Proportion of time when lowest elevation inundated [%]	Total time flooded
Median duration of a single flood at lowest elevation [days]	Flood duration med.
Maximum duration of a single river-wetland connection event [days]	Connection duration max.
Median length of time of a single connection river-wetland event [days]	Connection duration med.
Median month when mean elevation is inundated [month]*	Flood time med.
Month when mean elevation becomes dry (start of drawdown)[month]*	Drawdown start
<i>Response variables</i>	
Native species of Australia [%]	All natives
Terrestrial native non-weed species that inhabit dry areas of wetlands (water table below soil surface or soil saturated) [%]	T native non-weeds
Amphibious native non-weed species that inhabit wet-dry ecotone and require inundation some stage in life cycle [%]†	A native non-weeds
Terrestrial native weed species (i.e. native to Australia but naturalized or invasive elsewhere in world) [%]	T native weeds
Amphibious native weed species [%]†	A native weeds
Exotic (non-native) species [%]	All exotics
Terrestrial exotic (non-native) species [%]	T exotic weeds
Amphibious exotic species [%]	A exotic weeds
10 species‡	
Native non-weeds – <i>Alternanthera denticulata</i> ^{Ta} R. Br.; <i>Eleocharis acuta</i> ^{AP} R. Br.§; <i>Juncus ingens</i> ^{AP} N.A. Wakef.§; <i>Pseudoraphis spinescens</i> ^{AP} (R. Br.) Vickery.	
Native weeds – <i>Myriophyllum crispatum</i> ^{AP} Orchard§; <i>Paspalum distichum</i> ^{AP} L.	
Exotic weeds – <i>Cynodon dactylon</i> ^{Tp} (L.) Pers.; <i>Cyperus eragrostis</i> ^{AP} Lam.§; <i>Hypochaeris radicata</i> ^{Ta} L.; <i>Ludwigia peploides</i> subsp. <i>montevidensis</i> ^{AP} (Spreng.) P.H. Raven.	

Units used to quantify original variables in square brackets; all variables log₁₀-transformed (value + 0.01 for EV, value + 0.1 for RV), except *not transformed, †binary transformed, §square-root transformed. Explanatory variables calculated over 10 year period; for analyses, all variables were represented by percentage change from pre- to post-regulation conditions. %, percentage of 3653 days in 10 year period; max., maximum; SE, standard error. Response variables: species origin and weed status follow Randall (2007); terrestrial/amphibious flood response groups follow Brock & Casanova (1997); %, proportion of total vegetation cover in wetland; ‡details for species are in Table S2. T, terrestrial; A, amphibious; P, perennial; a, annual.

and drawdown were calculated for both the pre- and post-regulation scenarios. To reduce multicollinearity (indicated by Pearson correlation coefficients), eight variables that indicated changes to the five flood parameters were selected for analyses from a possible 27 variables (Table 1). To solve the problem of zero values, the extent and direction of hydrological change (except changes in timing) were represented by:

$$\text{Hydrological change} = \log_{10}(\text{post} + 0.01) / (\text{pre} + 0.01)$$

where post indicates post-regulation values and pre indicates pre-regulation values. For timing, change was the minimum number of months between pre- and post-regulation conditions represented by a percentage. If flood timing was delayed by 3 months, this was recorded as a 50% increase in timing, whereas floods that came 3 months early were considered a 50% decrease in timing.

FLORISTIC SURVEY

Wetlands were surveyed in the austral summer using a stratified random approach (13 December 2005–4 February 2006). Boundaries of wetlands were defined as the point where the elevational gradient became flat and where hydrophytes stopped occurring. Wetlands were divided into three strata based on elevation and water depth, which corresponded with vegetation zones at a site (Catford & Downes 2010). We used depth-strata to maximize sampling efficiency and

reduce residual error. Vegetation was surveyed at 24 random points in each wetland (eight points per depth-stratum). Points were generated in a Geographical Information System environment (Hawth's Analysis Tools: Beyer 2005) based on the floodplain DEM (MDBC 2001), and located in the field using a geographical positioning system (Garmin XL 12). At each sample point, a 1-m² square floating quadrat was blindly tossed. All taxa in the quadrat were recorded, and their foliar cover estimated using the Braun-Blanquet scale. Braun-Blanquet scale values were converted to mid-point averages for statistical analysis (Catford & Downes 2010).

Of 157 taxa recorded, 127 were identified to species-level; 139 to genera and 148 to family (Table S1, Supporting Information authority: Botanic Gardens Trust 2007). Information on species traits was sourced from the literature (see Table S1, Supporting Information). At the most, cover of all unidentified plant taxa (mostly daisies, grasses and seedlings) made up < 6% of wetland vegetation cover (mean = 1.8%). A few of the unidentified taxa may have been exotic, but their low cover makes it unlikely that their exclusion affected the results. Species were categorized into eight groups based on functional response to flooding (Brock & Casanova 1997), geographic origin and history of invasion (Randall 2007; Table 1 and Table S1, Supporting Information). We could not reliably distinguish between invasive and non-invasive exotic species, so refer to all of them as exotic weeds. Mean foliar cover of the eight groups was calculated as a proportion of total cover for each wetland (24 quadrats/wetland,

Table 1). Data from the three depth-strata were given equal weight despite differences in their areal extent. The 10 species selected for analysis were the most prevalent and abundant taxa overall (Table S2, Supporting Information). Species' absolute cover was highly correlated with their cover as a proportion of total vegetation cover ($p > 0.951$), so – for ease of interpretation – absolute cover was used in the analysis.

STATISTICAL ANALYSIS

Correlation analysis (Pearson product-moment) was performed to exclude highly correlated variables ($p > 0.5$) from regression analysis. We used ordinary least squares bivariate linear regressions to examine relationships between floristic cover (18 variables) and hydrological change (eight variables; Quinn & Keough 2002). Scatter plots indicated that relationships were primarily linear (quadratic and cubic functions were unsuitable), and polynomial analyses did not improve explanatory power and hence were not used. Most variables required log- or square root-transformations (Table 1). Variables dominated by zeros were transformed into presence/absence data. Approximately seven significant results from the 144 bivariate regressions would be expected by chance alone ($\alpha = 0.05$), although each individual test was motivated to test our hypotheses. When interpreting the results, we therefore concentrate on relationships that are most compelling as adjudged by the strength and consistency of effects of hydrological change on flora.

To test whether flora responded more strongly to a combination of variables indicating hydrological change or to modification of a single variable, we compared results from bivariate and multiple regression analyses. Variables for inclusion in the multiple regressions were selected using best subsets regression analysis (Hamilton Walk procedure; Minitab 15 Statistical Software). While minimizing the likelihood of collinearity in additive models, best subsets regression identified complementary explanatory variables that most parsimoniously explained variation in proportional cover of exotic/native groups. Of the multiple best subset models provided for each response variable, one or two optimal models were selected based on adjusted r^2 and Mallows's C_p (Quinn & Keough 2002).

Using the subset of explanatory variables selected by the best subset models, multiple linear regressions were performed to determine floristic responses to the combination of variables. Even when explanatory variables were centred or standardized, parameter tolerances were too low (< 0.1) to interpret their individual effects in full models (Quinn & Keough 2002). We therefore report overall results of the additive models. Additive models have higher degrees of freedom, so may overestimate significance and adjusted r^2 values compared to models that include interaction terms. SYSTAT 12 was used for multiple regression models (Version 12.00.09, SYSTAT Software Inc. 2007, Chicago, IL, USA). Minitab 15 was used to perform all other analyses (Minitab Solutions: Minitab 15 Statistical Software). Alpha was set as 0.05 in all tests.

Results

ABUNDANCE OF PLANT GROUPS

Averaged across the 24 wetlands, native non-weed cover accounted for 49% of vegetation cover, 76% of which was made up of amphibious species. Native weed cover made up 23% of total cover, 76% of which was also amphibious. In contrast, amphibious exotic species made up 27% of exotic

Table 2. Characteristics of the native non-weed, native weed and exotic weed species pools

Characteristics	Native non-weeds	Native weeds	Exotic weeds
Family richness	24	14	21
Species richness	67	20	57
Forb (%)	53.7	55.0	70.2
Graminoid (%)	46.3	35.0	24.6
Clonal (%)	52.2	60.0	24.6
Terrestrial (%)	56.7	55.0	89.5
Amphibious (%)	43.2	45.0	10.5
Perennial (%)	83.6	65.0	38.6
Annual & Biennial (%)	11.9	25.0	71.9
Annual (%)	10.4	20.0	59.6

species cover, which averaged 18% of total cover across the study wetlands. There were similar numbers of terrestrial and amphibious native species (49 and 38 species respectively), whereas exotics were dominated by terrestrial species (51 and 6 species respectively; Table 2). The exotic/native groups were present in all sites with the exception of terrestrial native weeds (23/24 sites), amphibious native weeds (22/24) and amphibious exotic weeds (22/24). The 10 study species were observed in 15 sites on average (Table S2, Supporting Information). The two native weed species generally had higher maximum (63%) and mean absolute cover (18%) than the native non-weed and exotic weed species, but differences were not significant (2-sample t -tests, results not reported).

HYDROLOGICAL MODIFICATION

The extent of hydrological modification varied among wetlands (Fig. 3, Table S3, Supporting Information). Most hydrological variables only changed in one (a negative) direc-

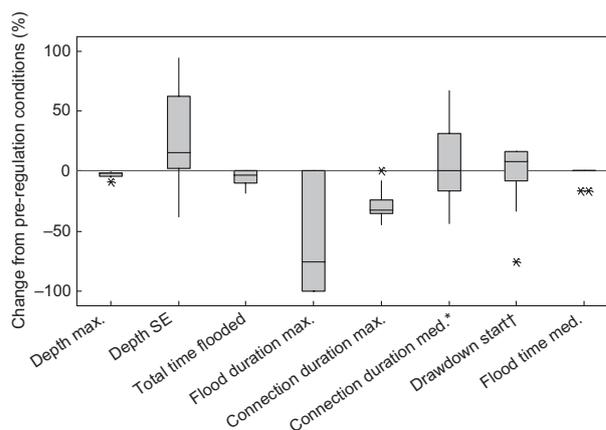


Fig. 3. Interquartile box plots showing percentage change in values from pre- to post-regulation conditions of eight hydrological variables in 24 wetlands. Calculated as: Change = $100 \times ((\text{post-pre})/\text{pre})$.

*Median connection duration increased by 985% at one site; outlier not shown in graph; †change in drawdown start is based on 11 sites.

Table 3. Significant bivariate regression models between floristic response variables and explanatory variables (absent variables lacked significant relationships; intercepts excluded)

Response variable	Model	Adjusted r^2
All natives	~6.17 Depth max.	0.164*†
A native non-weeds	~757 Depth max. ~-118 Connection duration max. ~14.5 Drawdown start	0.150* 0.203* 0.185*
All exotics	~-30.2 Depth max.	0.294**
T exotic weeds	~-38.2 Depth max.	0.368**
<i>A. denticulata</i> ‡	~7.52 Depth SE	0.211*
<i>E. acuta</i> ‡	~110 Depth max.	0.285**
<i>J. ingens</i> ‡	~-127 Depth max.	0.220*
<i>P. spinescens</i> ‡	~91.6 Depth max.	0.256**
<i>M. crispatum</i> ¶	~112 Depth max.	0.211*
<i>P. distichum</i> ¶	~9.84 Connection duration max.	0.170*†
<i>C. eragrostis</i> §	~12.4 Total time flooded	0.169*

* $P < 0.05$, ** $P < 0.01$; †relationship became non-significant with removal of outliers; ‡native non-weed; §exotic weed; ¶native weed; see Table 1 for transformations.

tion after regulation, thereby limiting the ability to test our hypotheses across the full range of possible changes, as depicted in Fig. 1. Overall, flood duration became shorter and wetlands were connected to the river for less time. Maximum flood depth (magnitude) decreased, but depth variability increased.

INFLUENCE OF HYDROLOGICAL MODIFICATION ON PLANT ABUNDANCE

Proportional cover of amphibious native non-weeds was the response variable most strongly related to hydrological modification (Table 3 and Table S4, Supporting Information). Under historical conditions, its proportional cover took a wide range of values, but as hydrological modification intensified, its cover decreased, as illustrated in its response to the reduction in maximum flood depth (Fig. 4). Amphibious native non-weed cover increased as wetlands were connected to the river for less time, and as the timing of drawdown changed. Three variables accounted for 62% of variation in amphibious native non-weed cover. Amphibious native non-weeds made up 51% of all native cover, and their response probably drove the relationship between hydrological modification and the group containing all native species (49% of variation explained; Table S4, Supporting Information). Change in maximum connection duration was not included in the best subset model for amphibious native non-weed cover even though it accounted for 20% of variation on its own. Among individual species, native non-weed species also had the strongest response to hydrological modification (Table 3 and Table S4, Supporting Information), followed by native weed species. Individual exotic species only showed a weak response.

Despite the negligible response of individual exotic species, 40% of variation in proportional cover of terrestrial exotic weeds (as a group) was accounted for by three hydrological variables. Terrestrial exotic cover increased

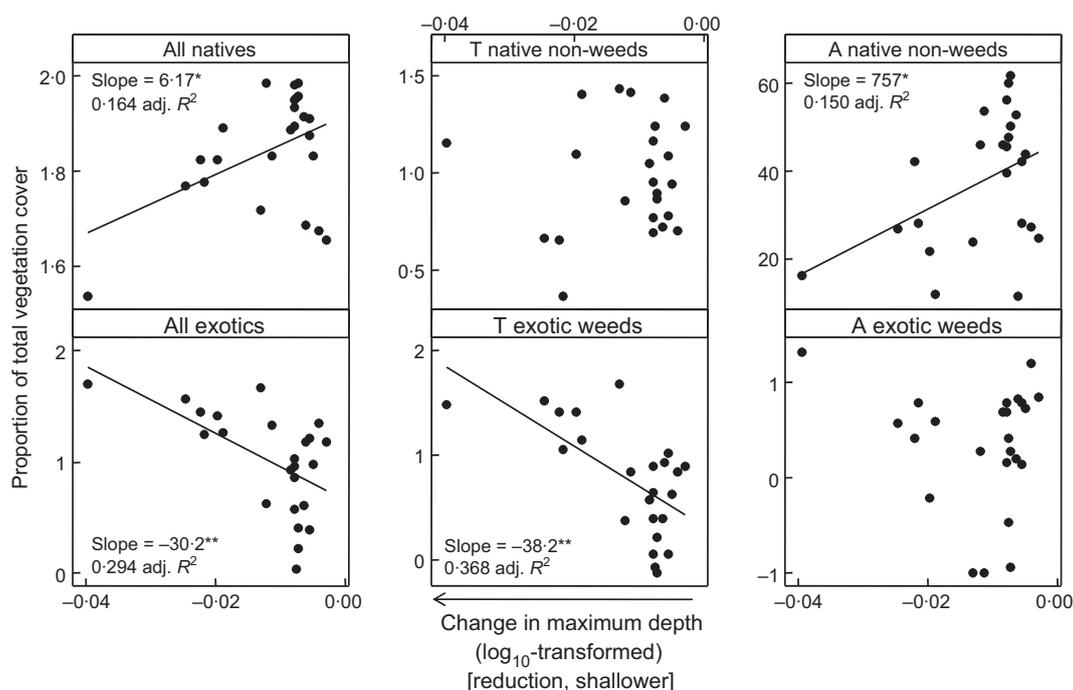


Fig. 4. Relationship between cover of exotic/native groups as a proportion of total vegetation cover and change in maximum wetland depth. Zero on the x-axes indicates no change from pre-regulation conditions. Responses of native weeds were non-significant (not shown). All variables were \log_{10} -transformed except amphibious native non-weeds; slope, regression coefficient; other details follow Table 3.

with a reduction in maximum flood depth (Fig. 4). Its relationship to hydrological modification was only slightly stronger than that shown by all exotic species, which reflects that terrestrial exotic species made up 73% of exotic cover. The proportional cover of both terrestrial native species groups did not relate to hydrological modification (based on *P* values, Table S4, Supporting Information), even though individual terrestrial native species did (e.g. *Alternanthera denticulata*). As a group, amphibious native weed cover was only related to hydrological modification when variables were combined.

Maximum depth had the strongest relationship with floristic cover of all explanatory variables (included in 8/18 bivariate regressions and 12/18 best subsets regressions), even though it changed the least between pre- and post-regulation conditions (~3% mean reduction = 0.14 m; Table 3, Tables S3 and S4, Supporting Information). Because maximum depth only changed in one direction, we can only compare the results to the left side of the graphs in Fig. 1. Responses to the reduction in maximum flood depth (i.e. magnitude) followed both Fig. 1a,b: proportional cover of terrestrial exotic weeds increased, amphibious native non-weed cover decreased, and native weed cover did not vary as maximum depth became shallower after regulation (Fig. 4). Like the amphibious native non-weed group, cover of *Eleocharis acuta*, *Pseudoraphis spinescens* and *Myriophyllum crispatum* decreased with a reduction in maximum depth, but *Juncus ingens* increased (Table 3).

The multiple regression models revealed that combined changes in hydrology accounted for greater variation in floristic cover than changes in isolation, as predicted. However, there were no specific combinations of hydrological variables that were consistently influential: the floristic variables were related to a variety of hydrological variable combinations (Table S4, Supporting Information).

IMPLICATIONS OF HIGHER PROPORTIONAL COVER OF EXOTIC SPECIES

The exotic species pool was dominated by species that are terrestrial, have a forb growth form, reproduce by seeds, and are annual or biennial (Table 2). In contrast, the native species groups were dominated by perennial species, but had similar proportions of terrestrial and amphibious species, forbs and graminoids, and species that have the capacity to reproduce vegetatively and those that do not. Consistent with the species pool trends, proportional cover of exotic weeds was negatively correlated to several measures of wetland vegetation diversity while native cover was positively correlated with them (Fig. 5). Notably, wetlands with a higher proportion of native non-weed cover had higher total species diversity (i.e. all species, not just native species), whereas wetlands with higher proportional cover of exotic species had lower species evenness (Fig. 5). The diversity of plant species' heights, time of flowering, and months in flower were not strongly correlated with any of the native/exotic groups.

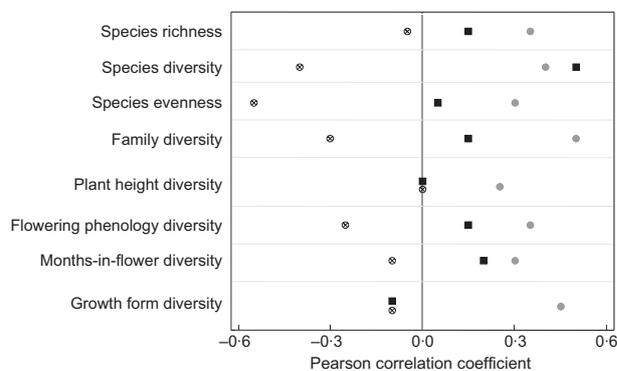


Fig. 5. Correlations between measures of 24 wetlands' floristic diversity and wetlands' proportional cover of native non-weeds (black squares), native weeds (grey circles) and exotic weeds (crossed circles). Diversity measures were calculated using the Shannon Weiner index; flowering phenology refers to the start of flowering; growth form includes trees and shrubs, graminoids, forbs.

Discussion

Using a novel comparison of modelled pre- and post-regulation hydrology, we have shown that flow regulation affected plant community composition and diversity in 24 River Murray wetlands. As predicted, exotic cover was highest and native non-weed cover lowest in wetlands that had experienced the greatest change in hydrology, namely a reduction in the largest flood event in the 10-year period modelled. The trends were driven by a decline in amphibious native non-weed cover and an increase in terrestrial exotic weed cover. By reducing flows to floodplain ecosystems, river regulation may prompt such a shift towards a more terrestrial flora (Deiller, Walter & Tremolieres 2001). However, in line with our ideas of habitat specialists and generalists, the decline in native non-weed cover with hydrological modification, increase in exotic weed cover but a lack of response from the native weed groups suggests that flow regulation altered the environmental filters of these wetlands in more ways than just causing 'terrestrialization'. Notwithstanding the unidirectional change in hydrology, the results appear to support both Hypothesis 1 and 2: by altering habitat filters, hydrological modification caused a reduction in native non-weed species cover and simultaneously provided drier conditions that directly favoured the exotic species group dominated by terrestrial species. Exotic species were potentially further assisted by human-mediated dispersal.

WHY WAS THE TERRESTRIAL EXOTIC SPECIES GROUP SO SUCCESSFUL?

Neither 'specialist' nor 'generalist' terrestrial native species cover increased as flood magnitude and depth reduced post-regulation. While the response of specialist native non-weeds is consistent with Hypothesis 1, the distinct responses of native weed and exotic weed cover implies that the success of the exotic weeds was not reliant on their 'weedy', generalist characteristics. Rather, the increase in exotic cover may reflect that

the majority of exotic species (but not the most prevalent or abundant, i.e. *Hypochaeris radicata* and *Cynodon dactylon*) were specifically adapted to the new conditions – invoking Hypothesis 2 (Fig. 1b).

Any changes that made wetlands drier would have advantaged the exotic species group as almost 90% of its species were terrestrial. The lack of functional diversity and dominance of terrestrial species in the exotic species pool probably stems from propagule bias (i.e. an introductory bias towards species with particular traits: Colautti, Grigorovich & MacIsaac 2006), which is not surprising given that most would have been introduced for local agriculture and horticulture, reflecting broader trends (Randall 2007). Unlike amphibious plants, which are rarely introduced deliberately, terrestrial species may be planted for landscaping, pasture improvement and land rehabilitation (Hulme *et al.* 2008), which would elevate both their propagule numbers and richness. A large species pool is more likely to contain a competitive dominant than a small one (Tilman, Lehman & Thomson 1997), but individual dominant species may have a greater influence than species richness on total abundance of invaders (Crawley *et al.* 1999). Therefore, despite the small numbers of amphibious exotics, they have the potential to constitute a large proportion of total cover, and some are currently spreading in the region [e.g. *Sagittaria platyphylla* (Engelm.) J.G. Sm.], if not already abundant (e.g. *Ludwigia peploides* subsp. *montevicensis*). Hypothetically, and in accordance with Hypothesis 1, it is possible that amphibious exotic cover would have increased instead of terrestrial exotic cover if conditions had become wetter rather than drier post-regulation. However, because most hydrological variables only changed in one direction (which is logical given the river supplies irrigation water), we cannot ascertain whether exotic species are especially well-adapted to the modified conditions or whether their higher cover in particular wetlands relates to other factors, like human-mediated propagule pressure or their novel evolutionary histories.

Exotic species' distinct evolutionary histories can enable favourable biotic interactions, like enemy release (Keane & Crawley 2002), but the study wetlands were probably too large for these effects to be detected. Evidence from multiple systems suggests that exotic plant invasion will be concentrated around areas of human activity, probably as a response to elevated propagule pressure (Botham *et al.* 2009). In the study region, wetlands that experienced greatest reductions in flood magnitude were typically close to towns ($\rho = 0.487$), and terrestrial exotic cover was higher in these areas (bivariate regression slope = -0.0454 , $P = 0.01$, adjusted $r^2 = 0.234$; native cover was unaffected). Exotic cover was also higher near roads, human settlements and agricultural land (J.A. Catford, unpublished data). This association with human activities – and particularly towns – may partially explain why terrestrial exotic cover increased ahead of terrestrial native cover in sites most affected by flow regulation. Owing to the close proximity of towns to rivers and the prevalence of exotic vegetation around human settlements, human-mediated propagule pressure is thought to contribute to the high levels of invasion in riparian ecosystems (Richardson *et al.* 2007). Propagule pressure of

exotic species can be reduced by replacing exotic pasture or garden plants with native varieties, disposing of green waste appropriately (e.g. compost, garden and aquarium plants), and maintaining sufficient buffer widths between urban or agricultural land and riparian zones (also see Sheley, Mullin & Fay 1995).

IMPACT OF FLOW REGULATION ON WETLANDS' FLORISTIC DIVERSITY

Hydrological modification did not directly affect floristic diversity of the wetlands at the time of the survey (the authors, unpublished data). However, wetland diversity was generally higher when native species were more abundant and lower when exotic species made up a greater proportion of total cover (Fig. 5). By altering the balance between native and exotic species groups that have different functional characteristics (Table 2), flow regulation may impair the ecological function of these riparian wetlands over time (Kyle & Leishman 2009). For instance, because the majority of exotic species have an annual life history – in contrast to the perennial-dominated native species pool – an increase in proportional cover of exotic species may lead to changes in resource availability and local abiotic conditions (Holmes & Rice 1996), and impede community resilience to environmental perturbations (Lavorel *et al.* 1997). Indeed, the capacity of a community to maintain its ecological function is often tied to its functional composition rather than its species diversity (Mayfield *et al.* 2010).

EFFECTS OF HYDROLOGICAL MODIFICATION ON WETLAND FLORA AND MANAGEMENT IMPLICATIONS

Corresponding with findings elsewhere (Deiller, Walter & Tremolieres 2001; Elder 2003), a reduction in flooding following flow regulation has altered the composition of River Murray floodplain vegetation. We found that terrestrial exotic species were abundant in areas formerly unsuitable for terrestrial species (other than for short periods) thanks to a reduction in the magnitude of peak flows (8.5–18 year ARI under pre-regulation conditions, which occurred in October 1996). Change in maximum flood depth was the most influential hydrological variable, and was more strongly related to exotic cover than proximity to human activities or other factors associated with riparian invasion (e.g. grazing intensity, soil nutrient levels, habitat heterogeneity: Catford 2008). Although the proportional decrease in maximum depth was minor compared to changes in other hydrological variables, depth can control wetland plant establishment and survival (Budelsky & Galatowitsch 2000) and average differences of 0.14 m in water depth (i.e. mean decrease on maximum depth) are large for individual plants. More importantly though, the reduction in flood magnitude effectively meant that there was a reduction in wetland area that was inundated: a greater proportion remained dry. This drier environment was suitable for terrestrial species, most of which were exotic.

Flow regulation has led to riverine ecosystems becoming more terrestrial throughout the world, but especially in large floodplain rivers in temperate climates (Dynesius & Nilsson 1994). The shift towards drier conditions has given terrestrial species an opportunity to invade floodplain areas that were previously unsuitable. Introduced plant species are typically good colonizers that can exploit the high levels of resource availability characteristic of riparian zones (Rejmánek & Richardson 1996; Richardson *et al.* 2007). Reflecting their introduction histories (e.g. for agriculture, landscaping), most invading species are not specifically adapted to riparian zones and cannot withstand flooding, as this study (Table S1, Supporting Information) and other studies illustrate (Décamp, Planty-Tabacchi & Tabacchi 1995; Deiller, Walter & Tremolieres 2001). The two observations – that regulated rivers are generally becoming drier, and that the success of most introduced plants relies on minimal inundation – highlights the potential for managing terrestrial weeds with flooding.

Akin to using fire as a weed management tool (Lonsdale & Miller 1993), inundating areas dominated by terrestrial weeds should kill much of the standing crop and, in doing so, may place native and exotic species on a more level playing field. While terrestrial exotic species will no doubt establish between floods, inundation will ensure that terrestrial exotic species do not dominate wetlands for decades at a time, and will provide an opportunity for native wetland plants to regenerate and disperse. Exotic plant propagules may also be dispersed by floodwaters (Howell & Benson 2000). However, a study that examined the spatial structure of these plant communities found no evidence that hydrochory (water-borne dispersal) influenced the abundance of exotic flora (Catford & Downes 2010). This would in part reflect that most of the exotic species are terrestrial and do not use hydrochory.

Although water abstraction and diversion means that most riverine ecosystems are getting drier overall, ample opportunity remains for amphibious species to invade, as invasion by *Phragmites australis* in North America attests (Hudon, Gagnon & Jean 2005). Species adapted to riparian zones differ in their hydrological preferences, so if flood regime management is used to control amphibious weeds, specific species must be targeted: 'one size' does not fit all (Mortenson & Weisberg 2010). *Sagittaria platyphylla* arguably poses the greatest threat to River Murray wetlands at present (DPI 2009), so implementing a flood regime that disadvantages this invasive species may be a priority. Preliminary evidence suggests that fluctuating wetland water levels and allowing wetlands to drawdown in summer would be effective control strategies (J.A. Catford, unpublished data). Rather than an alternative, such a strategy would be complementary to the one that addresses terrestrial weeds, though the spatial and temporal scales of implementation may differ.

Water regimes are made up of numerous interdependent parameters, and our study confirms that wetland plants are affected by the flood regime as a whole. However, in this section of the River Murray, if a management aim was to provide conditions that favour native non-weeds over the current pool of exotic species, environmental water should principally be

used to reinstate the magnitude of mid-range flow events, rather than flood frequency or flood duration. To simulate events equivalent to those observed in our 10 year study period, this would involve raising discharge above 113 000 ML day⁻¹ at Corowa and 160 000 ML day⁻¹ at Tocumwal for at least two consecutive days (rates of change in discharge should mimic the natural hydrograph, so discharge should be elevated for ≥6 days). Reintroducing a range of flood magnitudes will ensure that wetlands located at different heights on the floodplain are inundated. This will limit the degree to which terrestrial weeds dominate drier areas of the floodplain. We therefore recommend that flows equivalent to 10–20 year ARI under pre-regulation conditions are restored along this section of the River Murray (Corowa: 117 000–131 000 ML day⁻¹; Tocumwal: 147 000–163 000 ML day⁻¹).

While our findings indicate that the timing of these flows is not crucial, we recommend that environmental water be used to augment 'natural' floods that typically occur in spring. By implementing these recommendations, other aspects of the water regime (e.g. total time inundated) will shift in a way that favours native species over exotic ones. Overall, our conclusions support one of the aims of hydrological rehabilitation of the River Murray – to facilitate recruitment of native wetland plants by increasing the magnitude and duration of flood events (MDBA 2009). However, our study shows that it is *flood magnitude*, rather than duration, that is most important for wetland flora.

Environmental flows are being used to ameliorate impacts of flow regulation in rivers around the world (Poff *et al.* 1997). Given that environmental water allocations are typically limited, it is essential that release decisions are robust and science-based. Studies, like this one, that examine the response of biota to specific hydrological parameters may indicate which aspect – if any – of the flow regime is most important and what type of release will be of greatest ecological value. Integrating findings from studies that collectively examine biophysical and ecological responses to hydrological modification can help guide the delivery of environmental water (Arthington & Pusey 2003). By examining vegetation responses to different aspects of hydrological modification, we have shown that restoring the magnitude of peak flood events in regulated rivers should help maintain the functional composition of floodplain vegetation and limit invasion by terrestrial weeds.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Map of the 24 study wetlands.

Appendix S1. Details of the wetland water balance models including model evaluation.

Table S1. Information about all plant taxa observed in the study wetlands, including their prevalence and cover.

Table S2. Classification details, foliar cover and prevalence of the 10 species analysed (the most abundant and prevalent taxa in survey).

Table S3. Descriptive statistics of eight flood regime variables under pre- and post-regulation conditions, and percentage change in values from pre- to post-regulation conditions.

Table S4. Results of best subsets multiple linear regressions for the proportional cover of exotic/native groups and absolute cover of 10 species using eight hydrological change variables.

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