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Recruitment of a keystone tree species must concurrently manage flooding and browsing

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Running head: Multiple pressures on tree recruitment

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Summary

1. Multiple pressures (land-use change, water extraction and climate change) interact to influence biodiversity and ecosystem processes, but direct evidence for interactions among multiple pressures is limited. Floodplain forests are an acute example of how interacting pressures (river regulation, water extraction, decreasing rainfall, mammal browsing) interact to degrade native ecosystems.

2. We conducted a 2-year field experiment to determine how flooding, browsing and sediment salinity interacted to determine *in situ* seedling survival and growth of the keystone floodplain tree species (*Eucalyptus camaldulensis* Dehnh.). On semi-arid floodplains of southern Australia, 1-year-old seedlings were planted on the banks of six ephemeral creeks, three of which were flooded with management flows before planting while the others remained dry. Four plots were established at each creek, two open to browsing and two fenced to exclude mammal herbivores.

3. Flooding had a strong positive effect on seedling survival and height but browsing had strong negative effects. Sediment salinity (a covariate rather than a designed effect) had a weak negative effect on seedling survival and height.

4. The positive effects of flooding were largely offset by the negative interaction with browsing and, to a lesser extent, sediment salinity.

5. Although flooding has been restored to some degraded floodplain forests subjected to river regulation and a drying climate, the long-term success of such actions is likely to be undermined by persistent browsing.

6. *Synthesis and applications.* Management actions that focus on single pressures (e.g. infrequent flooding) and processes (e.g. mature tree survival) while ignoring other pressures are unlikely to sustain populations of keystone species, suggesting that complementary strategies (managed flooding with herbivore control) are necessary to sustain recruitment and, therefore, ensure the future health of these essential ecosystems.

Introduction

Floodplains have been changed drastically through land clearance and water extraction for human use (Grafton *et al.* 2013). Many floodplain ecosystems experience more pressure from climate change (Grafton *et al.* 2013) and it is uncertain how much these pressures may interact (Capon *et al*. 2013), but they are at least likely to be additive (Selwood, McGeoch & Mac Nally 2015). River regulation and water extraction often reduce the frequency, magnitude and duration of flooding, disrupting connectivity among rivers, floodplains and aquifers (Tockner & Stanford 2002). Reduced flooding greatly affects the structure and function of floodplain vegetation (Leyer 2005; Bino *et al.* 2015).

Up to 90% of some floodplains in the northern hemisphere have been cleared or degraded, mainly for agriculture (Tockner & Stanford 2002). The future of remaining floodplain forests depends on the successful recruitment of new trees, which is controlled by climate, flooding and geomorphology (Osterkamp & Hupp 2010) and by biotic processes, including competition and animal browsing (Horner *et al.* 2010). For long-lived trees, the effect of these pressures changes with age (Kendall *et al.* 2011). Trees are most susceptible to pressures such as drought as seedlings because seedlings have limited reserves (Merritt *et al.* 2010). Understanding the factors that limit seedling survival is essential for predicting recruitment and long-term population viability of floodplain forests in the face of multiple, interacting pressures (Shafroth, Stromberg & Patten 2002).

Floodplain tree seedlings often face three interrelated pressures: browsing, flooding (or lack thereof) and salinization, each of which has been altered by human actions and climate change (Mac Nally *et al.* 2011). River regulation reduces the frequency and extent of flooding and, therefore, limits forest productivity (Robertson, Bacon & Heagney 2001). Forest condition has declined on many lowland floodplains from altered groundwater availability or salinization (Cunningham *et al.* 2011). Mammal browsing reduces seedling survival, which induces changes in forest structure and composition (Jansen & Robertson 2001). Native herbivores greatly reduce recruitment of floodplain trees in conservation areas because herbivores are ‘confined’ to these remnants and may thrive from reduced predation (Painter *et al.* 2015).

Most studies of floodplains have not evaluated the interactive effects of multiple pressures (Jones & Sharitz 1998). Synergistic effects may be more important than individual effects in modifying floodplain forests (Brook, Sodhi & Bradshaw 2008). Reduced flooding frequency increases water stress on seedlings and vulnerability to drought and browsing mortality. Infrequent and restricted flooding in dry periods can lead to the concentration of herbivores into areas with water (Robertson & Rowling 2000). Extensive clearance of vegetation in many arid river basins alters hydrological balance and raises saline water tables. River regulation exacerbates salinization by reducing the frequency of flooding and the leaching of salt from floodplains (Jolly, McEwan & Holland 2008).

Here, we considered the floodplain forests of the Murray-Darling Basin (MDB) as an exemplar of how multiple pressures (altered flooding, browsing and salinization) affect seedling recruitment in floodplain ecosystems. The MDB is the most important agricultural area in Australia, covering 14% of Australia's land mass (1.1×10^6 km^2) (Pigram 2007). Floodplain vegetation of the MDB has a dynamic structure and composition due to hydrological patterns (Bino *et al.* 2015), and is disproportionately important for conservation of terrestrial and aquatic species (Selwood *et al.* 2015). Floodplain forests declined drastically since European settlement in the 1780s from changes in land and water use. Historically, flooding was frequent and widespread across the MDB but is now rarer and less pronounced (Mac Nally *et al.* 2011). Rapid, sustained increases in temperatures, record low rainfall and inflows into river systems, and increased frequency and severity of projected droughts under future climates (IPCC 2014) are superimposed on two centuries of regional-scale land clearance in the MDB (Camilleri, Thomson & Mac Nally 2010).

River red gum *Eucalyptus camaldulensis* Dehnh. is the dominant floodplain tree of the southern MDB and is a keystone species providing the main habitat structure for a diverse biota (Mac Nally *et al.* 2011). There has been extensive dieback of floodplain forests (100 000s ha) since the late 1980s from altered flooding regimes, drought and salinization (Cunningham *et al.* 2009). This forest dieback is associated with dramatic changes in the composition of these floodplains (Lada *et al.* 2008; Horner *et al.* 2012; Mac Nally *et al.* 2014). In response to the dieback, management agencies have embarked on artificial inundations, or 'managed flooding'. We took advantage of this floodplain-scale manipulation to measure the factors that regulate recruitment success of this keystone tree species.

We conducted a field experiment on the survival and growth of seedlings of *E. camaldulensis* subjected to different combinations of interacting pressures. We asked: do managed floods enhance survival of tree seedlings? How might potential benefits of flooding for seedlings be affected by browsing or sediment salinity? This information will determine whether complementary strategies (managed flooding with herbivore control) are necessary to sustain recruitment and, therefore, to ensure the health of these essential ecosystems.

Materials and methods

STUDY AREA

The experiment was carried out on two anabranch islands of Australia's major river, the Murray River, Lindsay Island (34°10'S 141°10'E) and Wallpolla Island (34°10'S 141°45'E) (Fig. 1). The region is semi-arid with a seasonally uniform rainfall of 262 mm yr^{-1} and mean annual evaporation of ca 1800 mm yr^{-1}, hot summers (mean maximum January temperature = 32.1 °C, Lake Victoria Storage 1922-2015, BOM 2015) and mild winters (mean maximum July temperature = 15.3 °C, Lake Victoria Storage 1922-2015, BOM 2015). The experiment was conducted from 2006 to 2008 towards the end of the 'Big Dry' (1997–2010), which included some of hottest years on record (mean annual maximum of 25.2 °C compared with the long-term average of 23.8 °C).

We deliberately selected some of the more westerly, xeric floodplains of the Murray River because conditions in these forests provide projections for the future of the more easterly, and currently more extensive and mesic, floodplain forests under a drying climate (Mac Nally *et al.* 2011). The experiments involved combinations of managed flooding and browsing, taking into account sediment salinity as a covariate. The browsing treatment was considered to be indicative of the future browsing regime given the ongoing recovery of feral rabbit *Oryctolagus cuniculus* L. populations after rabbit haemorrhagic disease (Lawrence 2009), the increased abundance of native herbivores [kangaroos *Macropus fuliginosus* (Desmarest) and *M. rufus* (Desmarest)] in conservation reserves (Morgan & Pegler 2010) and continuing livestock grazing (NRC 2009). The flooding treatment was regarded as the potential future hydrological regime given that managed flooding is being used to sustain the health of floodplain forests in the absence of natural flooding. Unlike natural flooding, managed floods are over small areas (100s of ha) and durations (<3 months) due to the limited water available for this purpose.

The study floodplain is up to 12-km wide (Fig. 1), with river flows entering and leaving the floodplain through networks of ephemeral creeks. The floodplain sediments are deep-cracking clays and sandy-alluvial loams. Typical salt concentrations in river flows ranged between 130–160 μS cm^{-1} during the study, while the adjacent floodplain was underlain by highly saline groundwater of 20 000–70 000 μS cm^{-1}, at depths of 2–4 m (Cunningham *et al.* 2011).

Banks of the ephemeral creeks support riparian forests dominated by *Eucalyptus camaldulensis*, with subdominant smaller trees (*E. largiflorens* F.Muell. and *Acacia stenophylla* A. Cunn. ex Benth.), shrubs, grasses and forbs (Horner *et al.* 2012). Canopy height ranged from 15–30 m and mean live basal area was 29.3 ± 2.8 SD m^2 ha^{-1}. *Eucalyptus camaldulensis* can produce large crops (up to 37 kg $tree^{-1}$, Jacobs 1955) of small seeds (1–1.5 mm diameter), which are buoyant and can be dispersed long distances in slow-moving (ca 4 km h^{-1}) floods. Livestock (sheep and cattle) were introduced to the floodplains in the 1840s with as many as 25 000 sheep during the 1950s. The floodplain largely has been destocked since the creation of Murray-Sunset National Park in 1991, but several hundred sheep still graze the eastern end of the study area. In the 1890s, rabbits became abundant, adding to the browsing pressure from livestock and native kangaroos.

FIELD EXPERIMENTS

In September 2006 (austral spring), 480 seedlings of *E. camaldulensis* were planted in 24 plots on the banks of six ephemeral creeks, three of which were artificially flooded for 6–8 weeks. Managed flooding was engineered by pumping water from the river into dry anabranch creeks that were dammed at their entrances using levee banks. Maximum flood depth among plots ranged from 0.4–0.7 m.

Two pairs of browsed and unbrowsed (1 × 2 m) plots were established along each creek. Browsing treatments (browsed or unbrowsed) were allocated randomly within each pair of plots, with all mammal herbivores being excluded by 1.3 m high steel fencing, with wire netting (3 cm mesh) attached.

One-year-old seedlings, grown from seed collected from a Murray River floodplain with similar climate and hydrological conditions (ca 80 km downstream from the study area), were obtained from a commercial nursery. Twenty seedlings were planted 40 cm apart in each plot. Seedling survival and height were measured eight times (spanning two austral summers) between October 2006 and June 2008 (0, 61, 151, 182, 273, 365, 578 and 609 days after planting).

In the austral spring of 2007, we collected three sediment cores from each plot at 20–30 cm below the surface, which corresponded to the lower seedling root zone. Sediment salinity was estimated by measuring electrical conductivity from the sediment samples using the 1:5 sediment/water paste extraction method (Rayment & Higginson 1992).

STATISTICAL ANALYSES

The effects of flooding, browsing and sediment salinity on seedling survival were analysed by fitting an interval-censored, Weibull survival model (Bartolucci, Bae & Singh 2008) with random plot and site effects. An interval-censored model was used because the time of mortality was not known precisely, but fell in the interval between two sampling times. Survival models were fitted using Bayesian inference, which is useful for fitting hierarchical models such as interval-censored survival models with random effects (Wong, Lam & Lo 2006). The Weibull survival function gives the probability that the time of death of an individual, T, exceeds time t:

$$P(T > t) = \exp\left(-(t/\alpha)^{\gamma}\right); t \geq 0, \gamma, \alpha > 0. \qquad \text{(eqn 1)}$$

Here, α is the scale, or characteristic survival, parameter and γ is the Weibull shape parameter. The time of death T is treated as an unknown variable with the Weibull distribution truncated to the interval (t_{lower}, t_{upper}), where t_{lower} is the last time a plant was recorded as alive and t_{upper} is the first time it was recorded as dead (Wong, Lam & Lo 2006). We modelled α as a function of treatment levels, salinity, and plot-level and site-level random effects:

$$\log\left(a_i\right) = \beta_0 + \beta_1\, flood_i + \beta_2 browsing_i + \beta_3\, flood_i \times browsing + \beta_4 salinity_i + \varepsilon_{plot[i]} + \varsigma_{site[i]}$$

Here, *flood* and *browsing* are binary indicator variables (0 = unflooded or unbrowsed; 1 = flooded or browsed), and *salinity* is the standardized $[\,(x_i - \bar{x})\,/\,\mathrm{SD}(x)\,]$ sediment salinity at 20–30 cm depth; the intercept β_0 determines the survival rate in unflooded and unbrowsed plots at the mean salinity; β_1 is the flooding effect; β_2 is the browsing effect; β_3 is the interaction between browsing and flooding; β_4 is the salinity regression coefficient; and ε and ς are plot-level and site-level random effects, respectively.

There was no prior knowledge about treatment effects, so uninformative normal prior distributions (0 mean, high variance) were assigned to treatment effects, and exchangeable normal priors (Gelman & Hill 2006) to the plot- and site-level error terms:

$$\beta_j \sim N(0,10000), j=1,..,4; \varepsilon_j \sim N(0,\sigma^2_{plot}), j=1,\dots,Nplots; \varsigma_j \sim N(0,\sigma^2_{site}), j=1,\dots,Nsites.$$

N() indicates a normal distribution, *Nplots* is the number of plots, and *Nsites* is the number of sites. We used uniform priors for the standard deviations of the random effects (Gelman & Hill 2006) and a gamma prior for the Weibull shape parameter:

$$\sigma_{plot} \sim Uniform(0,10); \sigma_{site} \sim Uniform(0,10); \gamma \sim Gamma(0.001,1000).$$

This model was fitted using three chains each of 200 000 iterations (100 000 burn-in iterations; results discarded) implemented in WinBUGS vers. 1.4 (Spiegelhalter *et al.* 2002). Model convergence was assessed by examining chain-history plots and Rubin–Gelman–Brooks statistics (Gelman & Hill 2006).

The effects of flooding, browsing and sediment salinity on trends in seedling height were modelled by fitting a mixed Poisson regression model with random plot and site effects:

$$\begin{aligned} &H_i \sim Poisson(\lambda_{ij}) \\ &\log(\lambda_{ij}) = \alpha + (\beta_0 + \beta_1\, flood_i + \beta_2 browsing_i + \beta_3\, flood_i \times browsing) \times t_j + .\gamma salinity_i + \\ &\varepsilon_{plot[i]} + \varsigma_{site[i]}. \end{aligned} \qquad (3)$$

Here, α is the intercept, time is number of days since planting, the βs are trend parameters (e.g. the rate of change in unflooded, browsed plots is given by exp(β_0 + β_2)), γ is the linear salinity effect, and ε and ζ are plot and site random intercepts. An initial model fitted with treatment-specific intercepts confirmed that seedling height did not vary among treatments at planting (time = 0).

Results

Flooding had a strong positive effect on the survival of *Eucalyptus camaldulensis* seedlings, while browsing and sediment salinity decreased survival times (Table 1, Fig 2a). Flooding increased survival times nearly eight-fold in unbrowsed treatments [posterior means (95% credible interval, CI)] = 1934 (407–7685) days in flooded/unbrowsed treatments vs. 248 (75–976) days in unflooded/unbrowsed (posterior means are modelled survival times). The flooding effect in the browsed treatments was marginally weaker, with an estimated 4.5-fold increase in survival times [310 (67–1507) days in flooded/browsed treatments vs. 76 (18–273) days in unflooded/browsed treatments]. However, similar flooding effects in browsed and unbrowsed treatments cannot be ruled out because the flooding × browsing interaction had large uncertainty (Table 1) and there was large overlap in the confidence intervals for survival times among treatments. Browsing reduced survival times by 83% in flooded treatments and a one standard deviation increase in sediment salinity (8 822 $\mu S\,cm^{-1}$) reduced survival times by 34% (Table 1).

Flooding before planting greatly increased height growth, such that at the end of the experiment (609 d) seedling height was 65 ± 10 cm in the unbrowsed/flooded treatment but only 5 ± 3 cm in the unbrowsed/unflooded treatment (Fig. 2b). Browsing reduced the height of seedlings (Table 2, Fig. 2b), with seedling height in the browsed/flooded treatment of 5 ± 4 cm being similar to that in the unbrowsed/unflooded treatment at the end of the experiment (Fig. 2b). In the browsed/unflooded treatment, seedling height was reduced rapidly and browsed to ground level by the end of the experiment (Fig. 2b). In the unflooded treatment, browsing reduced total seedling height by 99% yr^{-1} compared with 68% yr^{-1} for unbrowsed seedlings. In the flooded treatment, the total height of browsed seedlings was reduced by 77% yr^{-1}, compared with a 10% yr^{-1} reduction for unbrowsed seedlings (Fig. 2b). The average height reduction in the unbrowsed treatment was an artefact of size-specific mortality that occurred during the second summer (post-370 days, Fig. 2b). There was weak evidence that increasing sediment salinity reduced seedling height, but the effect was uncertain (Table 2).

Managed flooding had a strong positive effect on seedling survival and height while browsing substantially decreased survival and height (Table 1, Fig 2a). There was evidence of a negative effect of sediment salinity on seedling survival, but limited evidence for a negative effect on height.

Discussion

Managed flooding had a strong positive effect on seedling recruitment of *E. camaldulensis* on this semi-arid floodplain (Fig. 2, Tables 1 and 2). Browsing had a strong negative effect on recruitment, with the positive effect of flooding almost eliminated when seedlings were exposed to browsing by livestock and feral and native herbivores. Sediment salinity had a weaker negative effect on seedling survival and a negligible effect on seedling height. These outcomes have important implications for the recruitment of this keystone tree species, given reduced flooding due to river regulation (Nevill 2009), increasing floodplain salinity (Cunningham *et al.* 2009), increasing frequency and severity of droughts (Verdon-Kidd & Kiem 2009), and ongoing browsing by livestock and other herbivores on many floodplains (NRC 2009). Recent management of these forests has focused on flooding to arrest the dieback of mature trees. While a general program of more frequent flooding may increase seedling recruitment, without a strategy to address other interacting pressures, such as browsing, flooding alone will not ensure the long-term viability of these forests.

MANAGED FLOODING IMPROVES RECRUITMENT

The field experiment demonstrated the importance of managed flooding during dry periods for the successful recruitment of floodplain trees (Fig. 2, Table 1). Flooding is a critical process for seedling recruitment of *E. camaldulensis* elsewhere on the Murray-Darling Basin (Dexter 1978) and for other floodplain trees around the world (e.g. Karrenberg, Edwards & Kollmann 2002). Reduced flooding under river regulation often favours exotic trees and herbaceous terrestrial weeds (e.g. Merritt & Poff 2010; Catford *et al.* 2011). Notwithstanding differences in the hydrologic, geomorphic and climatic context between upland and lowland floodplain forests, hydrologic connectivity between a river and its floodplain appears to be fundamental for seedling recruitment (Streng, Glitzenstein & Harcombe 1989; Jones & Sharitz 1998). Prolific recruitment of floodplain tree seedlings often follows floods, which create germination sites by increasing soil moisture and in some cases improving access to shallow water tables and scouring previously occupied substrate (Mahoney & Rood 1998).

The timing of flood recession in relation to the growing season is important to germination and successful recruitment of seedlings. For *E. camaldulensis*, seedlings that germinate at the beginning of the growing season (e.g. end of the austral winter) are likely to have higher survival rates than those that germinate later because early germinants establish deeper root systems to access soil moisture during the first summer after germination when conditions are hot and dry (Dexter 1978). Similarly, on the arid floodplains of south-western North America, seedlings of many tree species germinate prolifically and early in the season minimizing exposure to browsing and avoiding desiccation (Streng, Glitzenstein & Harcombe 1989). Future predictions of reduced rainfall for many areas (IPCC 2014) will reduce flooding frequency, decreasing opportunities for seedling recruitment on floodplains (Rood *et al.* 2008). Managed flooding provides an important tool for mitigating the effects of human-induced drying by emulating historical early-season flooding to maximize recruitment success.

INTERACTION OF FLOODING AND BROWSING

Mammal herbivores affect recruitment of tree seedlings on floodplains because they may act as consumers (removing plants), parasites (browsing plants) or have mutualisms (distributing seeds and propagules, Crawley 1983). Flooding may modulate the effects of browsing by limiting foraging opportunities and herbivore population density or through affecting resource availability and physiological stress for tree seedlings (Andersen & Cooper 2000). An example of the impact of browsing is the near absence of recruitment of aspen *Populus tremuloides* Michx. in western North America from browsing by the Rocky Mountain elk *Cervus elaphus* L. Tree recruitment greatly increased following the reintroduction of elks' predator, the grey wolf (*Canis lupus*, L. Painter *et al.* 2015).

Our understanding of the direct effects of mammal herbivory on floodplains is limited because few studies have experimentally manipulated browsing and monitored seedling survival (e.g. Opperman & Merenlender 2000). Exclusion studies on floodplains in south-western North America showed substantial decreases in height growth (60%), density (90%) and survival (25-50%) when tree seedlings were unprotected from browsing during periods with some flooding (Andersen & Cooper 2000; Andersen 2005). Despite the positive effect of management flooding, mammal browsing greatly reduced survival rate (83%) and growth in height (92%) for tree unprotected seedlings (Fig. 2). This pronounced browsing effect probably is due to the experiment being conducted at a time of acute food shortage associated with the worst recorded drought in south-eastern Australia's history (van Dijk *et al.* 2013).

Flooding regime has important implications for browsing of tree seedlings and, therefore, for the successful recruitment of future floodplain forests. Floodwaters typically exclude most mammal herbivores from floodplain forests (apart from aquatic herbivores, such as beaver

Castor spp.), but river regulation often leads to an increase in the density of terrestrial herbivores (Andersen & Cooper 2000). Herbivores are attracted to the receding waters where there is more food. Floodplain forests in semi-arid regions are more prone to elevated browsing than adjacent upland vegetation because herbivores concentrate near water, particularly during droughts (Robertson & Rowling 2000). Water stress can make seedlings more nutritious to herbivores, particularly insects (Crawley 1983). River regulation has reduced flooding frequency, extending access to floodplains and the duration of browsing between floods. Persistent browsing, such as in the unfenced creeks in our study, leaves seedlings vulnerable to other pressures such as salinity, desiccation (Kozlowski 1997) and submergence by subsequent floods (Dexter 1978), while favouring other structural types (e.g. grasses and shrubs, Bakker *et al.* 2004). Our sampling did not allow us to measure herbivore densities or separate out species effects. However, there is evidence and observations of all three species (livestock, kangaroos and rabbits) contributing to browsing mortality across the floodplain (P. Kelly, pers. communication, May 2009). Hence, management actions that reduce browsing pressure from all mammal herbivores during the critical establishment phase (24 months after flooding) are recommended for enhancing seedling recruitment and the overall ecological value of managed flooding.

Given the predicted increased frequency of extreme drought (Hartmann *et al.* 2013), the substantial negative effects of browsing on recruitment of tree seedlings on floodplains may become increasingly typical, rather than exceptional, for many semi-arid and arid regions around the world. To reduce the negative impacts of browsing on tree seedling recruitment, managed floods should be extensive, to provide a widespread growth pulse that disperses herbivores across the floodplain, and more frequent to reduce browsing-induced seedling mortality between floods. Trade-offs are likely to occur when prescribing managed flood regimes for sustaining forest health. For example, flooding in successive years will enhance mature tree growth (Robertson, Bacon & Heagney 2001), but drown seedlings that germinated in response to the initial flood (Dexter 1978). If seedling recruitment is paramount, an inter-flood period of at least 24 months is needed for seedlings to reach sufficient height (>1 m tall) to tolerate subsequent flooding.

INTERACTION OF FLOODING AND SEDIMENT SALINITY

Salinity has become a significant problem on arid floodplains, such as the Murray River, because irrigation and catchment deforestation have elevated the naturally saline water table while river regulation has reduced the frequency of floods that formerly freshened sediments and rivers (Jolly, McEwan & Holland 2008). Forest dieback occurs when groundwater becomes unavailable to trees due to excessive salinity or depth (Cunningham *et al.* 2011). There is good understanding of the groundwater use (Mensforth *et al.* 1994; Snyder & Williams 2000) and salinity tolerance of established trees (e.g. Niknam & McComb 2000), but not of seedling recruitment. Most salinity-tolerance studies are glasshouse trials (e.g. Marcar *et al.* 2002) and are unlikely to reflect the tolerance of *in situ* seedlings subject to multiple interacting pressures in floodplain ecosystems.

Sediment salinity had a negative effect on the survival of seedlings and may have suppressed growth (Tables 1 and 2). The salinity effect was much smaller than the negative impacts of browsing, but we caution that sediment salinity was a covariate rather than a designed effect. Glasshouse trials have shown seedling growth of *E. camaldulensis* provenances is reduced by 43–82% when grown at the salt concentrations found in many of our collected sediments (ca 14 600 µS cm–1, Marcar *et al.* 2002). There are substantial growth reductions of seedlings of cottonwood *Populus fremontii* S. Watson and willow *Salix gooddingii* C. R. Ball from comparable floodplains in south-western North America (46% and 38%, respectively) at much lower salinities (8000 µS cm^{-1}) and death at sediment salinities > ca 16 000 µS cm^{-1} in glasshouse trials (ca 7800 µS cm^{-1}, Glenn *et al.* 1998). Our field experiment suggests that short-term inundation of seedlings (several weeks) may eliminate the negative effect of sediment salinity presumably by flushing salt from the rooting zone of the seedlings (Tables 1 and 2).

IMPLICATIONS FOR FUTURE MANAGEMENT OF FLOODPLAIN FORESTS

High mortality of mature trees due to a drying climate and river regulation (Horner *et al.* 2009) is important for land managers working with floodplain forests in semi-arid zones. However, the long-term viability of tree populations depends on successful recruitment, so there is an urgent need to increase seedling recruitment in many floodplain forests around the world.

Many studies have shown that patterns of establishment and growth in the earliest stages of forest development are critical in setting the trajectory for subsequent stand-level structure and composition (Horner *et al.* 2009). We focused on this early life stage recognizing that it is crucial for sustaining future forest structure and function. Seedling survival of *E. camaldulensis* was improved dramatically by managed flooding, but this improvement was abolished by mammal browsing (Fig. 2). Fortunately, most of the pressures controlling seedling recruitment can be addressed by active management, albeit for small areas given the limited water typically available for managed flooding in these water-stressed systems.

Understanding the complex interactions among pressures and use of integrated strategies (managed flooding with herbivore control) are necessary to sustain recruitment of *E. camaldulensis*, a keystone tree species in these floodplain ecosystems. Historical flooding regimes must be emulated (increased frequency of winter to early spring floods) to stimulate tree recruitment for long-term population viability. Current managed flooding in semi-arid Australia often is restricted to creeks and wetlands, leading to undesirable recruitment of trees. Floods should maximize the area of forest inundated to stimulate a widespread growth pulse (of tree seedlings and herbaceous understorey plants), reducing the concentration of herbivores and browsing-induced seedling mortality. Temporary fencing could be used to improve recruitment at small targeted locations (e.g. Edenius *et al.* 2011), and be removed once saplings have established and are less prone to browsing (height > 2 m, e.g. Harmer 2001).

The pressures of river regulation and browsing on floodplain forests are increasingly prevalent in floodplains around the world, including southern North America, China, the Middle East and Africa (Döll & Zhang 2010). While flooding is a key process affecting tree seedling establishment and survival, the reintroduction of historical flood regimes is a formidable challenge under the projected dramatic decreases in river flows (climate, human use) and accompanying increases in temperatures for many arid floodplain ecosystems (IPCC 2014). Most arid floodplains have become divided into small, isolated areas that receive managed floods at best, those that are flooded (rarely) during extreme floods, and the large remainder that may not be flooded again (Capon *et al.* 2013). The future of many floodplain forests is likely to be as small 'islands' of remnant forest where managed flooding occurs regularly enough within a broader landscape dominated by declining or dying forests (Selwood, Mac Nally & Thomson 2009). The adoption of flexible management practices that anticipate and accommodate future uncertainty will be critical for arresting declines in or sustaining floodplain ecosystem function

(Hulme 2005). At the heart of these efforts will be regular targeted floods in combination with suppression of browsing (e.g. temporary fencing) to maximize recruitment and maintain the structure of floodplain forests through extended dry periods.

Data accessibility

Experimental data (seedling survival, height and sediment salinity) have been registered with figshare doi: 10.6084/m9.figshare.1618656 (Horner *et al.* 2015).

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Table 1. Flooding, browsing and salinity effects in the survival model for seedlings. A proportional effect > 1 indicates increased survival (e.g. for flooding, survival was 7.7 times the control) whereas a proportional effect < 1 indicates decreased survival

Parameter	Coefficient	Mean ± SD	Proportional effect mean (95% CI)
Intercept	β_0	5.33 ± 1.05	–
Trends			
flooding	β_1	2.04 ± 1.27	7.70 (0.63, 92.1)
browsing	β_2	–1.28 ± 0.49	0.28 (0.11, 0.72)
flooding × browsing	β_3	–0.52 ± 0.66	0.60 (0.16, 2.17)
salinity	β_4	–0.42 ± 0.21	0.66 (0.43, 1.00)

Table 2. Flooding, browsing and salinity effects in the model of seedling height growth (cm y^{-1}). Coefficients are posterior means ± 1SD (95% CI). Rate column gives the % annual rate of change in height for each treatment combination, calculated as $100(e^{365.B/\gamma} - 1)$, where *B* is the sum of relevant standardized coefficients (e.g. $B = \beta_0 + \beta_2$ for browsed/unflooded treatment) and σ is the standard deviation of *time* (days since planting)

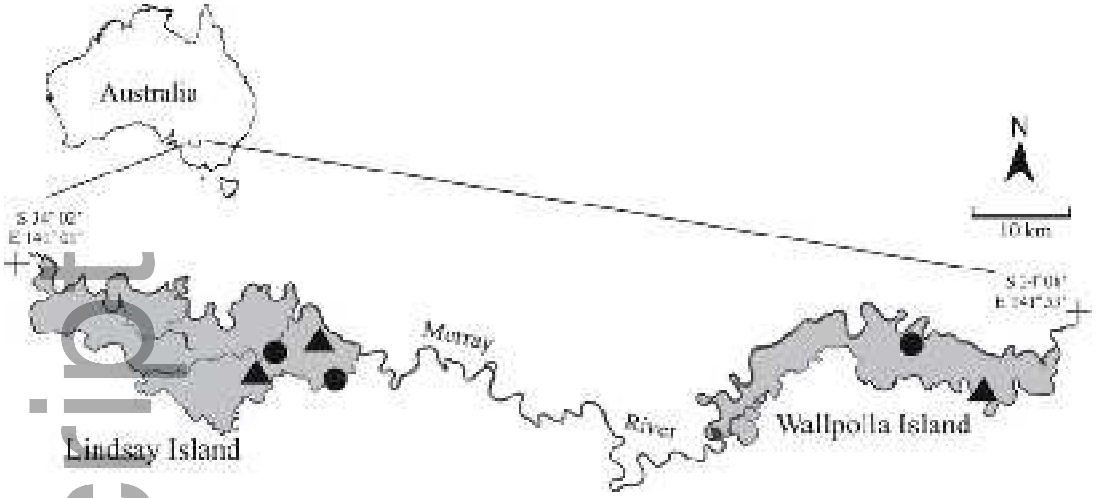
Parameter	Coefficient	Mean ± SD	95% CI	Rate (% yr^{-1})
Intercept	α	4.20 ± 0.26	(4.08, 4.78)	
Trends				
reference (β_0)	β_0	–1.14 ± 0.05	(–1.25, –1.04)	–68
flooding (β_1)	β_1	1.04 ± 0.06	(0.92, 1.16)	–10

browsing (β_2)	β_2	–3.34 ± 0.20	(–3.74, –2.96)	–99
flooding × browsing (β_3)	β_3	1.99 ± 0.21	(1.59, 2.40)	–77
salinity (γ)	β_4	–0.14 ± 0.10	(–0.33, 0.06)	

Figure legends

Figure 1 Location of the study area on the Murray River floodplain and of the sites across the creeks of this floodplain area. Symbols show the location of three flooded (▲) and three unflooded creeks (●). Grey shading indicates extent of historical floodplain.

Figure 2 Changes in survival (a) and height (b) of planted seedlings over time for the four flooding and browsing treatments: flooded/unbrowsed (▲), flooded/browsed (△), unflooded/unbrowsed (●) and unflooded/browsed (○).



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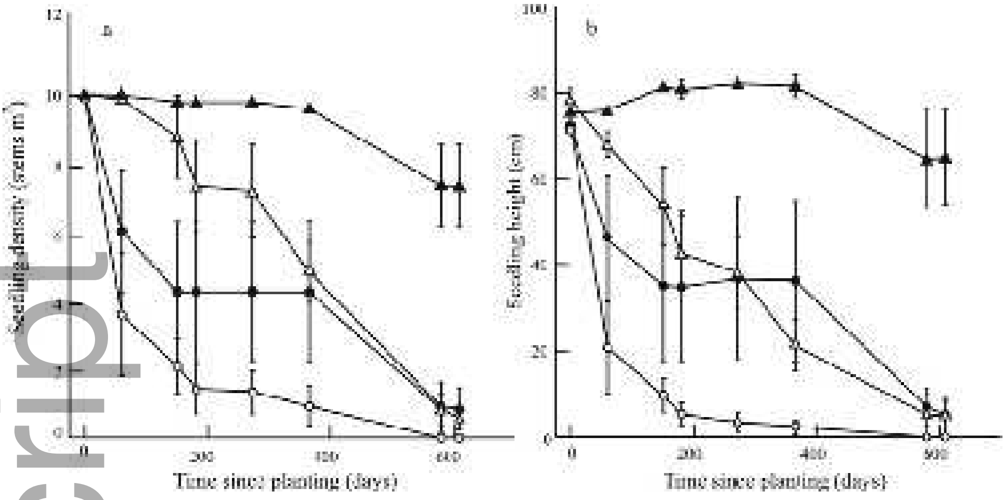

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