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Restored river-floodplain connectivity promotes riparian tree maintenance and recruitment

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ABSTRACT

Riparian forest loss and degradation due to river-floodplain disconnection is a global problem. Prospects for the maintenance and recruitment of riparian trees via restored flooding can be uncertain, in part due to competition from understorey vegetation and limited availability of tree propagules. In a field-based trial, we assessed the response of a keystone riparian tree to restored flooding, reduced competition and seed addition.

We built diversion weirs to reconnect floodplains supporting riparian forest. Using a multiple control-intervention-reference study design with two restored flooding (intervention) sites, two naturally-engaged (reference) and two dry (control) sites, we assessed seedling recruitment of the dominant tree, *Eucalyptus camphora*, with and without clearance of understorey vegetation and with and without seed addition. We also assessed the growth of extant trees using dendrometers and seedfall using funnel traps at all six sites.

Our weirs resulted in extensive flooding of the adjacent floodplain, while control sites remained dry. Flooding increased seed germination, seedling establishment, tree growth and seedfall. However, seed germination benefits were only realised where understorey vegetation was cleared and seed was added. Seedling establishment was also limited by dry summer conditions, except where flooding duration was longest (~6 months cf. < 3 months).

Restored flooding via river-floodplain reconnection is likely to promote the rehabilitation of riparian forests degraded by flow regulation or stream modification through benefits at multiple tree life-history stages. However, widespread tree recruitment may require complementary works that reduce competition via clearing of understorey vegetation and alleviate seed limitation by direct seeding or planting.

1. Introduction

Floodplain ecosystems rely on flooding for their productivity, structure and function (Junk et al. 1989). Many of the world's riparian forests are now in decline having become disconnected from their rivers because of human activities, such as river channelization and flow regulation (Bunn and Arthington 2002; Grill et al. 2019). Restoring river-floodplain connectivity and thus natural flood regimes should theoretically improve the condition of riparian forests (Poff et al. 1997). However, benefits from restoring natural flood regimes may be constrained by factors such as exotic plant invasion or limited propagule supply of the desired vegetation (Dawson et al. 2017). Field-based studies combining hydrological restoration and manipulation of other critical factors are required to improve our understanding of eco-hydrological relationships and ability to restore riparian forests (Brooks and Lake 2007).

Flood regime is critically important for riparian tree recruitment (Dixon 2003; Fischer et al. 2021). Many riparian tree species are adapted to germinate on moist sediments following flood recession (Mahoney and Rood 1998), and their recruitment can be precluded by a lack of flooding (Moxham et al. 2018). Nonetheless, factors such as competition from understorey vegetation, limited seed supply and grazing can also limit the recruitment of riparian trees (Meeson et al. 2002; Moxham and Dorrough 2008). The relative importance of flood regime, patches clear of understorey vegetation, and seed supply for riparian tree recruitment is uncertain (Andersen 1989; Moxham and Dorrough 2008).

Flooding can both inhibit or promote the growth of riparian trees (Dudek et al. 1998; Mitsch and Rust 1984). Seasonal or intermittent flooding is likely to provide better conditions for tree growth than prolonged or no flooding (Greet et al. 2020; Kozlowski 1997; Robertson

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et al. 2001; Vieira et al. 2005). Riparian tree growth responses to flooding may also be dependent on tree size and stand density (Allen et al. 2019; Greet et al. 2020), such that tree growth responses to restored flood regimes may be varied.

Flood regime also affects the reproductive output of riparian trees (Greet et al. 2020; Moxham et al. 2018). Many woody riparian species do not maintain a persistent soil seed bank and thus rely on recently released seeds for seedling recruitment (Greet 2016; Greet et al., 2012b). Such species often have phenologies adapted to natural flood regimes, which maximise potential for recruitment, e.g. seed release timing linked to flow recession or drawdown (Hamilton-Brown et al. 2009; Pettit and Froend 2001). Additionally, regular flooding may be important for riparian tree condition and their reproductive output, with trees in better condition producing more seed (Jensen et al. 2008; Moore et al. 2016; Moxham et al. 2018).

Here we test the potential of flood regime restoration to promote the rehabilitation of riparian forests. In a field-based experiment, we enhanced river-floodplain connectivity through diversion of channelised flows in conjunction with clearing of understorey vegetation and addition of propagules, and assessed the response of a keystone riparian tree species, *Eucalyptus camphora* R.T.Baker. We hypothesise that flood regime is the primary constraint for all life-history stages of riparian trees (reflecting adaptations to particular flood regimes: Catford and Jansson 2014; Greet et al., 2012a), with seed germination and seedling establishment further limited by competition from dense understorey vegetation and low propagule availability (Moxham and Dorrough 2008; Ruthrof et al. 2010; Yates et al. 2000) (Fig. 1). Specifically, we expected that restoring flooding would increase *E. camphora*: i) seed germination, ii) seedling establishment, iii) extant tree growth; and iv) seedfall. We also expected that seed germination and seedling establishment (i and ii) would be augmented by clearing understorey vegetation and adding seeds of *E. camphora.*

2. Materials and methods

2.1. Study site

Our study was conducted along the Macclesfield Creek floodplain within the Yellingbo Nature Conservation Reserve (Yellingbo NCR; 37° 51′ S, 145° 29′ E; c. 110 m ASL), south-eastern Australia (Fig. 2). The area has a temperate climate, experiences mean daily maximum temperatures of 13.6 °C in winter and 25.6 °C in summer and receives c. 1100 mm of rainfall annually. The reserve comprises c. 680 ha of remnant riparian and swamp forest along several watercourses including Macclesfield Creek, and is surrounded by cleared agricultural land.

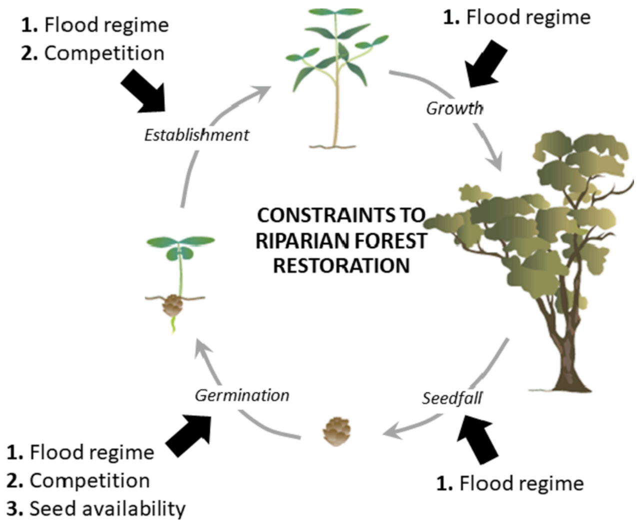

Fig. 1. Hypothesised primary constraints to riparian forest restoration at key life-history stages of riparian trees: 1) inappropriate flood regime can limit seed germination, plant establishment and growth, and seedfall; 2) interspecific competition with understorey vegetation limits seed germination and seedling establishment (collectively seedling recruitment); and 3) seed availability may limit the number of seeds that germinate.

The Macclesfield Creek floodplain within the reserve is dominated by swamp forests that are seasonally inundated, with *E. camphora* the sole dominant occurring as a continuous canopy or scattered emergent in association with paperbark (*Melaleuca* spp.) and tea-tree (*Leptospermum* spp.) thickets (McMahon and Franklin 1993). This community varies in structure from open forest to woodland with a variable canopy height (6–25 m) and supports a dense understorey of sedges, rushes, grasses and forbs (Turner 2003).

E. camphora swamp forests at Yellingbo represent the largest remnant of this forest type and provide habitat for the last remaining wild populations of helmeted honeyeater (*Lichenostomus melanops cassidix*, bird), and lowland Leadbeater's possum (*Gymnobelideus leadbeateri*, marsupial), both of which are critically endangered (Harley et al. 2005; Pearce and Minchin 2001). Where streams have been channelised (e.g. middle reaches of the Macclesfield Creek; Fig. 2), floodplains have been disconnected and the condition and regeneration of woody vegetation has putatively been impacted by reduced flooding (Boon 2016). Downstream reaches of the Macclesfield Creek are not channelised and comprise anastomosing channels that distribute water across floodplains supporting healthy swamp forest (Fig. 2).

2.2. Experimental design

To divert water into relict flood-runners and reengage disconnected floodplain areas, we built two small temporary weirs in September 2018. We built the diversion weirs using sandbags at two locations along a channelised section of the Macclesfield Creek within the Yellingbo Nature Conservation Reserve (Fig. 2). Both weirs were successful in raising water levels upstream of the weirs sufficiently to divert water from the channel into relict flood-runners and flood the Maccclesfield Creek floodplain downstream and adjacent to the channel, with surface water eventually draining back into the channel (Fig. 2). At each of these (intervention) sites, and at two corresponding unflooded (control) and two naturally-engaged (reference) sites, we established an 8-m × 8-m fenced plot (to exclude herbivores). At both of the intervention sites and within the reference area we set up Odyssey® Capacitance Water Level Loggers to monitor flooding levels in the creek and on the floodplain. Water levels were monitored in mm and logged every 15-min; both of the control sites remained dry during the experiment. At each of the six sites we assessed: the seed germination and seedling establishment of *E. camphora* within cleared and uncleared patches (within the fenced plots) and with and without seed addition, i.e. in a full factorial experiment; and the growth and seedfall of *E. camphora* trees. A schematic of the experimental design is provided in Supplimentary Material (Figure S1).

2.3. River-floodplain connectivity

Flooding at the reference sites occurred almost continuously from early July until mid-December 2018 to a maximum depth ~ 0.41 m (Figure S2). Both weirs successfully raised water levels sufficiently for water to spill from the channelised stream sections and flood the adjacent floodplain. In the first flooding season (2018). The extent and duration of floodplain engagement varied between the two sites due to microtopographical variation across the floodplain. At the upstream site (Intervention 1), flooding occurred for short durations on several occasions (maximum duration = 8 days, maximum depth ~ 0.24 m). At the downstream site (Intervention 2), flooding was more widespread and occurred almost continuously for ~ 3 months (maximum depth ~ 0.33 m). In the second season of flooding (winter/spring 2019), flooding

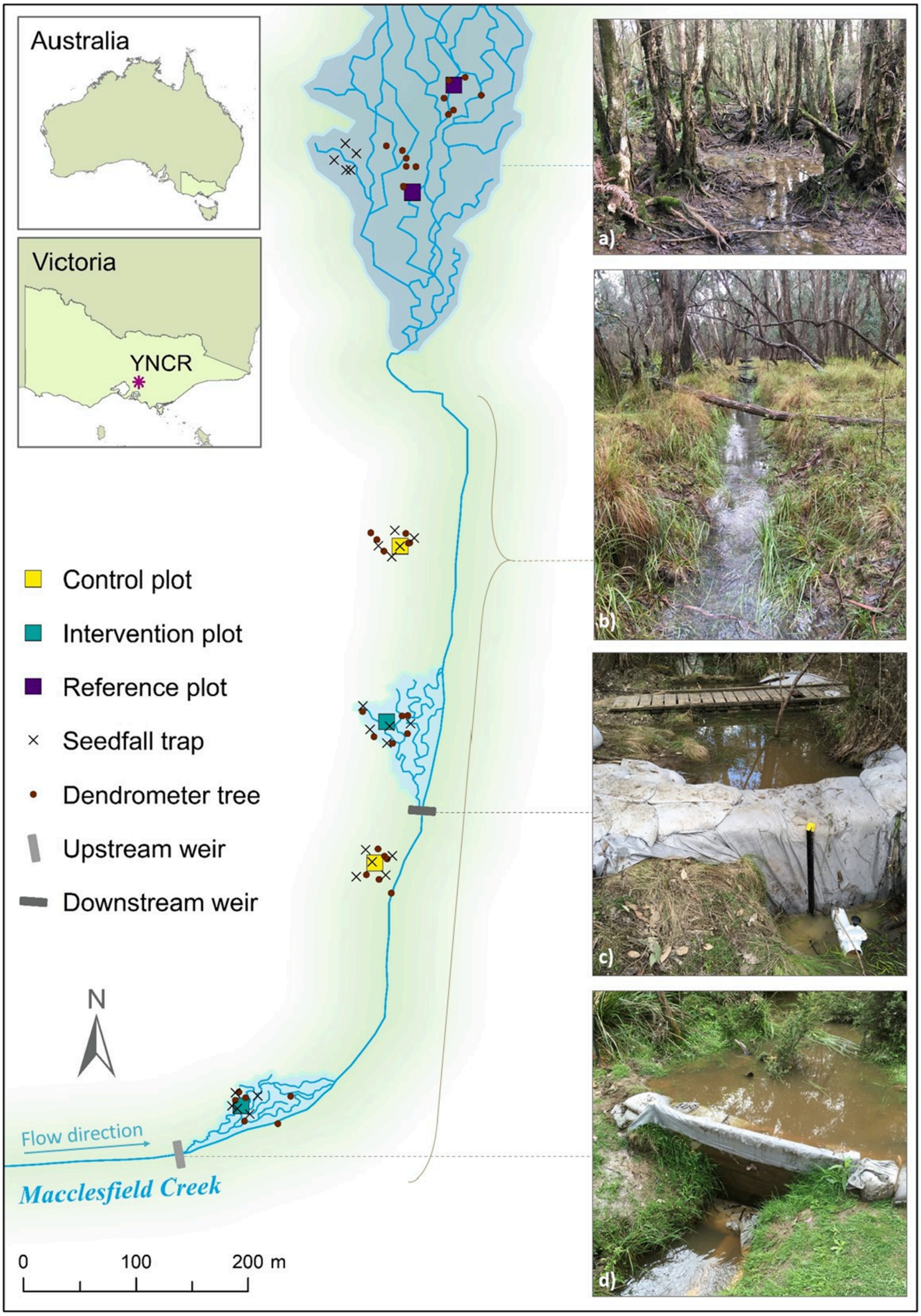

Fig. 2. Schematic of Macclesfield Creek study site showing the locations of flooding treatment plots, tree dendrometers and seedfall traps in relation to two diversion weirs built within a channelised section of the creek. The aim of the dieversion weirs was to reconnect adjacent floodplain areas within the Yellingbo Nature Conservation Reserve. There were 2 plots per flooding treatment (6 plots in total), and 5 dendrometer trees and 5 seedfall traps associated with each plot (30 in total for each). Within each plot, there were 20 patches used for the seed addition experiment (see Figures S1 and S3). Inset photos show a) unmodified downstream reference floodplain area with natural flooding via shallow anastomosing channels; b) channelised upstream section of the Macclesfield Creek comprising of a single incised channel; and c) downstream and d) upstream weir, both which raised water levels upstream of the weirs diverting flow into historic flood runners through which diverted water moves downstream on the floodplain, parallel to the incised channel.

durations were more similar across the reference and intervention sites, and flows generally higher than in 2018 due to higher rainfall (Figure S2).

2.4. Seed germination and seedling establishment

Using seed sourced locally (provided by Friends of Helmeted Honeyeater nursery; https://www.helmetedhoneyeater.org.au/nursery/), a 0.1-g sample of *E. camphora* seed was placed in each of 60 plastic vials. Each sample contained approximately 111 ± 5 viable seeds (mean ± standard deviation; determined using germination assays). To each sample one teaspoon (~5 g) of washed sand was added as a bulking agent. Within the fenced plot at each site, 20 randomly located 50-cm diameter circular patches were established in early December 2018. Half of the patches were cleared of above ground vegetation using a mattock and gently scalped using a rake-hoe. The remaining ten patches within each plot were left uncleared (Figure S3).

In mid-December, when surface water had just subsided, five each of the cleared and uncleared patches were sown with a sample of *E. camphora* seed (prepared as per above), giving a fully crossed design of four treatments: cleared, seeded; cleared, not seeded; uncleared, seeded; and uncleared, not seeded. Seed was sown onto the relevant treatment patches by sprinkling the seedlot samples by hand. No pre-treatment of seed was needed because *E. camphora* seeds are non-dormant and germinate readily.

Patches were surveyed for *E. camphora* seedlings (counted once both cotyledons had unfurled) at 3, 6, 12, 24 and 52-weeks post-seeding. During surveys at 3, 6 and 12 weeks, any tall (>50 mm) resprouting vegetation (typically sedges from rhizomes) in the cleared treatments was clipped close to ground level to maintain low-levels of above-ground competition. Hemispherical photos were taken in the centre of the four quadrants of each fenced plot at a height of 1 m to measure canopy cover (plant area index, PAI). Mean PAI ranged between 57 and 69% across sites and did not differ significantly between sites or flooding treatments and thus was not considered in our analyses.

2.5. Tree growth

At each site, we randomly selected six *E. camphora* trees (Fig. 2) that were > 10 cm diameter at breast height (DBH) and that formed part of the canopy (i.e. that were not sub-dominant). Selected trees ranged between 15 and 45 cm DBH. For each tree, we recorded the tree's initial size (DBH), and the distance to its four nearest neighbours to measure stand density using the point-centred quarter method (Cottam and Curtis 1956). That is, the distance to the nearest tree (>10 cm DBH) within each compass quadrant (NE, SE, SW, NW) and its DBH were recorded. We did this because tree growth responses to flooding have been shown to be dependent on tree size and stand density (Allen et al. 2019; Dicke and Toliver 1990). In early October 2018, we attached a manual band dendrometer (DBM80, ICT International, Armidale, Australia) to each selected tree at breast height (1.3 m) (Figure S4). Dendrometer measures of stem circumference to the nearest tenth of a mm were recorded initially (upon set up) and monthly thereafter for seventeen months (October 2018–April 2020).

2.6. Seedfall

Five seedfall traps were established at each intervention and control site, and at one of the reference sites (Fig. 2), on 1st of December 2018. One trap was set up centrally within the fenced plots used for the seeding experiment with the other four set up adjacent to the plot within ~ 5 m of each corner. Trap locations were haphazardly selected within pure *E. camphora* stands but not within 1 m of the trunk of any tree.

Seedfall traps comprised a plastic funnel (diameter 22 cm) with a fine mesh bag attached to its end sitting within a PVC pipe attached to a wooden stake (Figure S4). The bags were made of tulle fabric fine enough to retain seeds but permeable to water/moisture. Stakes were secured into the ground so that traps were ~ 1.3 m above the ground. For each trap, we identified the four nearest trees (using the point-centred quarter method as per above) and recorded their distance from the trap, size (DBH) and visually estimated their crown extent (proportion of existing branch structure supporting foliage; *sensu* Souter et al. 2009). Larger trees and those in better condition can be expected to have greater reproductive output (Greet et al. 2020; Jensen et al. 2008).

Seedfall traps were emptied monthly for the three austral summer months (December, January and February—peak periods of seedfall in *E. camphora*; Greet, J., unpublished data) in 2018/19 and 2019/20. At the end of each month, the mesh bag at the end of the funnel was collected and replaced. Any large material (leaves, sticks, etc.) within the funnel were brushed and removed, and smaller material collected in the sample bag. Samples were later placed in a drying oven at 30°C for 1 week and then sown over sterile seed raising mix and placed out into a temperature-controlled glasshouse. Sown samples were monitored for three months and numbers of emergent *E. camphora* seedlings recorded to determine seedfall.

2.7. Data analyses

We assessed the effects of flooding, clearing of understorey vegetation and seed addition on seed germination (seedling counts at three weeks) using a hierarchical linear regression where the number of seedlings in each patch were drawn from a Poisson distribution. The model included fixed categorical factors of flooding treatment (Control, Intervention, Reference), with two sites of each, clearing (yes or no) and seeding (yes or no), with five replicates of each clearing and seeding combination (i.e. 20 patches) at each site, and a random site effect. We compared two models, with and without an interaction term between clearing and seeding, and selected the simpler model as it was more parsimonious. Assessments of interactions between flooding treatment and either clearing or seeding were not possible due to too few sites.

We assessed the effect of flooding on tree growth (measured as the difference in stem circumference between readings) by month using a hierarchical linear regression assuming growth was normally distributed. The model included fixed categorical factors of flooding treatment, and month, and their interaction, and random effects for site and tree. We also assessed the effects of flooding, tree size and stand density on total tree growth across the eighteen months. This model included fixed factors of flooding treatment, tree size (DBH cm) and stand density (average nearest neighbour distance), and random effects for site and tree.

We assessed the effects of flooding, tree size, tree condition and stand density on seedfall during the summers of 2018/19 and 2019/20, separately. For each summer we modelled seedfall using a hierarchical linear regression assuming the numbers of fallen seeds in each trap were drawn from a Poisson distribution. The model included fixed factors of flooding treatment, tree size (DBH cm), tree condition (crown extent %), and stand density (average nearest neighbour distance), and a random site effect.

For all analyses we present boxplots or line graphs (as appropriate) of the raw data, and forest plots of model parameter estimates and confidence intervals for fixed effects of interest. We also provide tables of the the full results from the model outputs in Supplementary Material (Tables S1–S3). We fitted all models using the *lme4* package (Bates et al. 2015) in R version 3.6.0 (R Core team 2019). For all models, residuals were examined to ensure they fulfilled the assumptions of normality and homogeneity of variance. All data and code used for the analyses are freely available via the Open Science Framework (https://osf.io/vq7ac/).

3. Results

3.1. Seed germination

At three weeks, a median of 3 seeds (range 0–28) had germinated in patches that were cleared and seeded, with few seedlings emerging in patches receiving any other treatment combination (median = 0 for all other treatments) (Fig. 3a). Essentially, seedlings only emerged abundantly in cleared and seeded patches, and only at intervention and reference sites (Fig. 3a). Seed germination was 8.46 times greater in cleared than in uncleared patches (CI: 5.37–14.86) and 16.20 times greater in seeded than in not seeded patches (CI: 9.03–32.82) (Fig. 3b). Seedlings germination was 10.36 times greater at reference sites than control sites (CI: 1.14–299.16). While corresponding germination rates at intervention sites were estimated to be 5.79 times greater than that at control sites, given high uncertainties in these estimates due to low replication at the site level, this difference was not clear (CI: 0.56–149.39) (Fig. 3b).

3.2. Seedling establishment

Seedling establishment (survival to 52 weeks) was limited due to dry summer conditions in early 2019 (many seedlings were observed to desiccate during that period). After one year, seedlings only persisted at reference sites. Considering cleared and seeded patches only, a mean of 1 seedling established per patch (equivalent to ~ 5 seedlings per m^2) at reference sites (Fig. 3c).

3.3. Tree growth

Tree growth rates varied over time and were higher, on average, at intervention and reference sites than at control sites (mean growth rates = 35, 65 and 16 µm/day, respectively) in all months, except for January 2020 when rates were the same at control and intervention sites (Fig. 4a). Tree growth rates were initially high at both the intervention and reference sites when they were shallowly flooded, but not at control sites which remained dry. Growth was then negligible at all sites from December to March 2019 (and negative at control sites) during a particularly dry, summer period. Growth rates were higher at reference sites but similar at intervention and control sites during the spring and summer of 2019/2020, a period of above-average rainfall. Total tree growth over the seventeen months was not associated with tree size or stand density (Fig. 4b).

3.4. Seedfall

On average, seedfall rates were 36, 44 and 70 seeds/m^2 per month at control, intervention and reference sites, respectively, though rates did vary across years (Fig. 5a, b). *E. camphora* seedfall was seven times higher (7.07, CI: 2.85–21.95) at intervention sites than at control sites in the first summer following floodplain reconnection (2018/19), however, there were no clear differences in seedfall between flooding treatments in 2019/20 (Fig. 5a, b). *E. camphora* seedfall was not affected by either the mean tree size or condition (of neighbouring trees), or stand density, in either year (Figure S5).

4. Discussion

We found flooding to be critical for each of the four life-history stages studied of a keystone riparian tree species. As expected, flooding increased: i) seed germination, ii) seedling establishment, iii) tree growth, and iv) seedfall of the dominant riparian tree species. However, increases in seed germination were only realised where we also cleared understorey vegetation and added seed. Thus, seed germination is also constrained by competition and limited seed availability. Subsequent seedling establishment was also limited by dry summer conditions. Our results indicate that reinstating flooding via river-floodplain reconnection can promote the rehabilitation of riparian forests degraded via flow regulation or stream modification. However, widespread riparian forest regeneration is likely to require additional constraints to be alleviated.

4.1. Flooding increases seed germination and seedling establishment

Flooding clearly promoted seed germination from sown seed, with

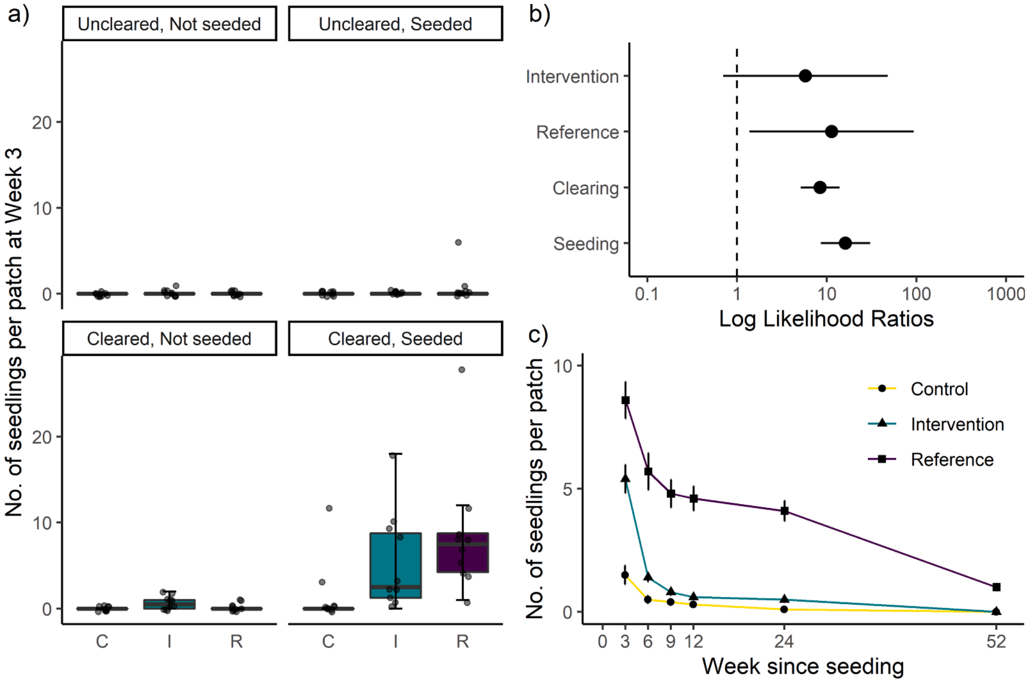

Fig. 3. (a), (b) seed germination, and c) seedling establishment across the different treatments: a) Boxplots of numbers of seedlings that had emerged per patch at week 3 across the four clearing and seedling treatment combinations, and three flooding treatments (C – Control; I – Intervention; R – Reference; n = 10 patches per clearing × seeding treatment combination for each flooding treatment). Bolded lines represent median values, boxes comprise the interquartile range (IQR: 25th to 75th percentiles) and whiskers comprise all data within 1.5 × IQR from the 25th to 75th percentiles. Grey circles represent raw data; b) Circles represent log-likelihodd ratios (exponents of model parameter estimates) ± 95 CIs for effects of flooding treatment (Intervention and Reference, relative to Ccontrols), clearing, and seeding on seedlings numbers; and c) Numbers of seedlings per patch by week since seeding across the different flooding treatments. N.B. only cleared, seeded patches considered as there was negligible establishment across all other treatment combinations. Means ± 1SE presented. See Table S1 for full model outputs.

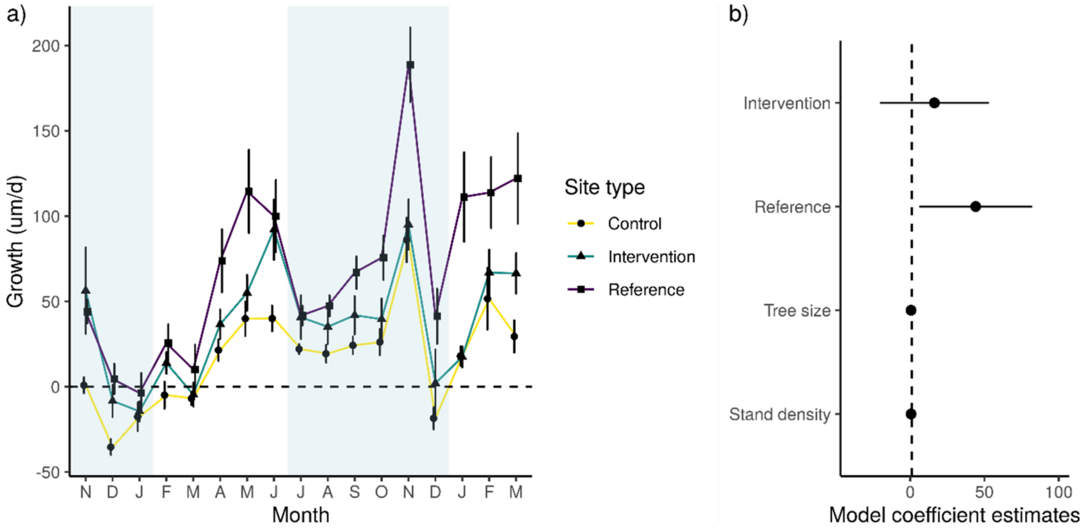

Fig. 4. a) *E. camphora* tree growth (increase or decrease in DBH μm/day) by month from October 2018 to Mar 2020. Approximate flooding periods at intervention and reference sites indicated in light blue; control sites remained unflooded. Means ± SE presented; b) Model coefficient estimates ± 95% CIs for effects of flooding treatment (Intervention and Reference, relative to controls), tree size (mean DBH) and stand density (mean nearest neighbour distance) on total growth over the 17 months. See Table S2 for full model outputs.

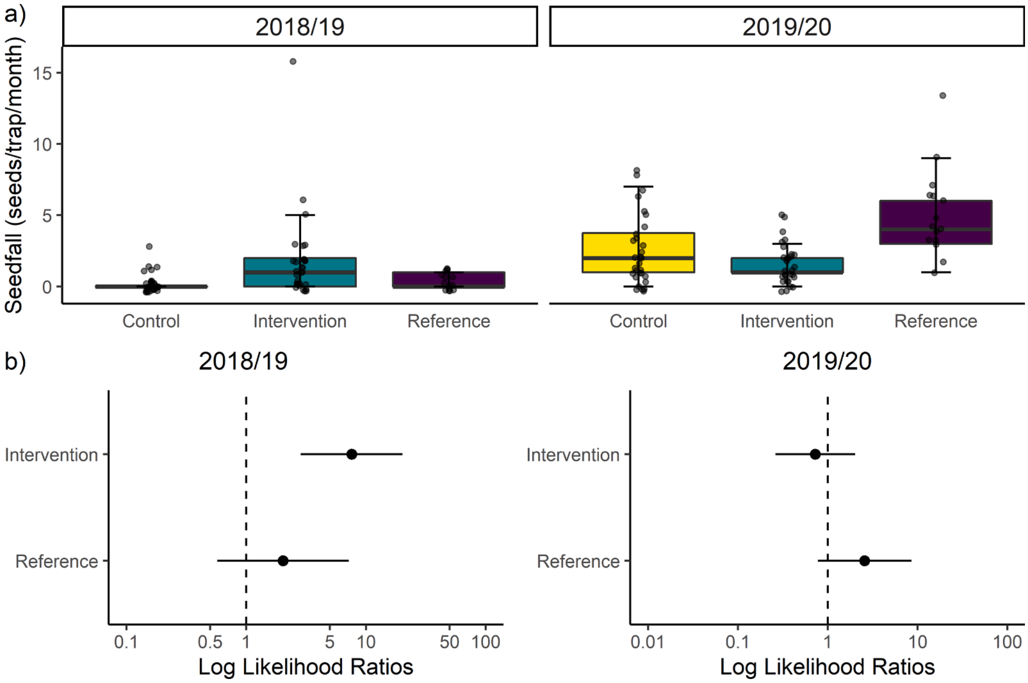

Fig. 5. a) Boxplots of numbers of *E. camphora* seeds caught in funnel traps each month over the three summer months (Dec, Jan, Feb) at control, intervention and reference sites in the first summer following initial floodplain reconnection (2018/19) and the following summer (2019/20). Bolded lines represent median values, boxes comprise the interquartile range (IQR: 25th to 75th percentiles) and whiskers comprise all data within 1.5 × IQR from the 25th to 75th percentiles. Grey circles represent raw data. b) Circles represent log-likelihood ratios (exponents of model parameter estimates) ± 95 CIs for effects of flooding treatment (Intervention and Reference, relative to controls), on seedfall in 2018/19 and 2019/20. See Table S3 for full model outputs.

few seedlings resulting from seed addition at unflooded sites. The higher moisture content of soils that had recently been flooded (at intervention and reference sites) likely favoured seed germination. This is unsurprising given that many woody riparian species require moist soils for seed germination (Jensen et al. 2008; Mahoney and Rood 1998; Stokes 2008).

Our study demonstrates that flooding alone may be insufficient to enable seed germination though. We only observed abundant germination at flooded sites where understorey vegetation was cleared and seed added. This is consistent with other studies of floodplain trees that have shown that seedling recruitment is strongly limited by competition and seed supply (Moxham and Dorrough 2008). Similarly, the recruitment of native forb species in temperate grasslands has been shown to be limited by both competition and seed availability (Johnson et al. 2018). In our experiment, a dense understorey of sedges, grasses and forbs is likely to have inihibited germination of *E. camphora* seeds. In other parts of the study area, dense stands of semi-aquatic clonal grasses, *Phragmites australis* and *Phalaris arundinacea*, also prevent seedling recruitment (Greet et al. 2016; Pearce 2000). Even where we cleared understory vegetation, germination was minimal without seed addition. Thus, while some studies of eucalypt species have suggested that the availability of bare soil, not seed supply, limits their recruitment (Andersen 1989), in our case, both were limiting.

Like others (Jensen et al. 2008; Streng et al. 1989), we also found evidence that the vagaries of local weather can limit seedling establishment of riparian trees. However, the harshness of dry conditions may be tempered by prior flooding. In our study, seedlings only reached 12 months old through a dry summer in areas that had experienced long duration flooding (∼6 months) beforehand. It is likely that it was only at these sites that soil moisture levels were sufficient for long enough for seedlings to establish (Fischer et al. 2021). Indeed, in the absence of flooding across multiple years, recruitment of riparian trees is often absent (Jensen et al. 2007; Moxham et al. 2018).

4.2. Flooding increases tree growth

In general, we observed tree growth rates to be negligible (or even negative at unflooded sites) during dry periods, and positive during periods of flooding or high rainfall. Thus, our results indicate that flooding is beneficial for riparian tree growth when rainfall is limiting. While prolonged flooding can reduce tree growth rates (Kozlowski 1986), as has been demonstrated for *E. camphora* for flooding durations > 200 days/year (Greet et al. 2020), the durations of flooding observed in this study (up to ∼ 6 months/year) increased tree growth. While tree growth responses to flooding can vary with tree size and stand density (Allen et al. 2019; Dicke and Toliver 1990), we selected trees of a similar size from sites with similar tree densities and hence these factors were not pertinent in our study.

4.3. Flooding increases seedfall

It has been suggested that flooding and subsequent drawdown acts as a trigger for seed release in woody riparian species (Hamilton-Brown et al. 2009). Our observations are consistent with this contention. Seedfall rates were seven times higher at our intervention sites following initial flooding (2018/19) than at nearby control sites that did not flood. However, these differences must be interpreted with caution. Seedfall rates the following summer (2019/20) were similar across all sites, despite differences in flooding patterns among sites being the same as the first summer. This suggests that inter-annual variability in seedfall may be comparable to the differences in seedfall observed between sites in the first summer. Indeed, seed production and seedfall patterns of eucalypts are cyclical, and also notoriously variable (Bassett 2002; Jensen et al. 2008; Keatley et al. 2021; Neyland et al. 2003; Vesk et al. 2010).

4.4. Implications for riparian forest restoration

Restoring river-floodplain connectivity is likely to promote riparian tree recruitment. While seedling recruitment was minimal at our intervention sites due to dry summer conditions in the first year, the high rates of seed germination in cleared and seeded patches and seedling establishment in cleared and seeded patches at reference sites (∼5 seedlings per m^2) demonstrate the potential that regular flooding provides for woody plant recruitment. We also suggest that the potential benefits of river-floodplain connectivity are greater than environmental flows/watering, as natural flood events are more likely to follow large rainfall events, thus maximising recharge of soil moisture and prospects for seedling recrutiment post-flooding (Streng et al. 1989; Fischer et al. 2021).

Our study demonstrates that efforts to restore riparian forests based solely on the return of more natural flood regimes may fail if other constraints are not managed concurrently, e.g. grazing (which was controlled for in our study via fencing), invasive plants and limited propagule availability (Meeson et al. 2002; Moxham and Dorrough 2008). Seedling recruitment is unlikely to occur in areas where understorey vegetation is dense or seed supply is limiting, even if those sites experience flooding. In such cases, widespread recruitment may require complementary works to reduce competition via clearing of understorey vegetation (likely exotic plant species in degraded systems) and plant introductions via direct seeding or planting.

Flooding is likely to promote tree growth, particularly in low rainfall areas or during drought periods. Trees can shrink in response to water-stress (as observed at our control sites in 2018), and successive years of diameter decreases are likely to lead to mortality (Bullock 1997; Pastur et al., 2007). It is likely that river-floodplain reconnection and regular flooding is vital for riparian tree and stand vigour long-term, while continued disconnection may ultimately result in tree deaths and forest loss (Catelotti et al. 2015; Moxham et al. 2018).

Our study provides tentative evidence that floods act as a trigger for seed release in riparian trees. Such trees are likely to be adapted to release seeds following flooding to take advantage of the favourable conditions for seedling recruitment (Hamilton-Brown et al. 2009). Regular flooding may also provide for higher seedfall rates via improved tree condition and reproductive output (Jensen et al. 2008; Moxham et al. 2018). In this study, trees at regularly flooded sites had higher average seedfall rates across the two summers of study. Thus, regular flooding can potentially boost seed supply via two mechanisms, as a trigger for seed release at opportune times, and via higher seed production rates longer-term. Nonetheless, the evidence provided by our study in support of these mechanisms is tentative, given the modest spatial and temporal scale of our study and the inherent variability in eucalypt seedfall. Regular flooding is nonetheless important to both maintain native soil seedbanks and disperse non-dormant seeds of woody riparian species (Dawson et al. 2017; Greet et al., 2012).

Our field-based experiment demonstrates that restored flooding achieved via river-floodplain reconnecton has the potential to rehabilitate riparian forests, with such flooding likely to benefit riparian trees via a range of responses including seed germination, seedling establishment, tree growth and sexual reproductive output. However, widespread woody plant recrutiment may require complementary works to reduce other constraints such as competition, via clearing of understorey vegetation, and seed supply limitations, via direct seeding or planting.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119952.

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