

# Native riparian plant species dominate the soil seedbank of in-channel geomorphic features of a regulated river

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Seedbank, restoration, environmental flows, fluvial geomorphology, riparian vegetation, ecosystem resilience

## Declarations

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The authors give consent for this research to be published.

All authors have been fully engaged in the development of the manuscript and agree to its submission in its current form. We also confirm that this manuscript has not been published elsewhere and is not under consideration by any other journal, and that we have no conflicts of interest to declare.

Study data is available via the Open Science Framework here: <https://osf.io/4vaew/>.

## 35 **Abstract**

36 Flow regulation impacts on riparian vegetation composition, often increasing the prevalence of  
37 exotic and terrestrial plant species. Environmental flows may benefit native riparian vegetation via  
38 the promotion of plant recruitment from riparian soil seedbanks, but this is dependent on an intact  
39 native seedbank. Thus, we assessed the composition of the soil seedbank of different riverine  
40 geomorphic features to determine its potential response to environmental flows.

41 Soil seedbank samples were taken from channel bars, benches and floodplains at six sites along the  
42 Campaspe River, Australia, a heavily regulated river that receives environmental flows. These  
43 geomorphic features represent a gradient in elevation and thus flooding frequency from frequently  
44 flooded (bars) to infrequently flooded (floodplain). Seedbank samples were 'grown out' in a  
45 glasshouse, and seedlings identified and classified according to taxa, flood tolerance and origin  
46 (native or exotic).

47 We identified 6515 seedlings across all geomorphic features and sites, with monocots most  
48 abundant. Soil seedbank composition varied between geomorphic features. Overall, seedling  
49 abundances were greater for in-channel features (bars and benches) than floodplains, but taxa  
50 richness did not vary likewise. Soil seedbanks of in-channel features were dominated by flood  
51 tolerant and native taxa, while flood intolerant and exotic taxa were generally associated with  
52 floodplains.

53 The dominance of native flood tolerant taxa in the soil seedbanks of in-channel geomorphic features  
54 suggest these seedbanks can play an important role in the resilience of native riparian plant  
55 communities. Moreover, environmental flows are likely to play a positive role in maintaining native  
56 riparian plant communities given such conditions.

## 57 **Introduction**

58 Few of the world's rivers remain free-flowing, with most now regulated (Grill et al. 2019). Flow  
59 regulation typically negatively impacts on native riparian vegetation (Nilsson and Svedmark 2002;  
60 Poff et al. 1997), often decreasing native plant species diversity (Greet et al. 2013) and increasing the  
61 prevalence of exotic plants (Catford et al. 2011, Catford et al. 2014), thus altering the composition of  
62 riparian plant communities (Bunn and Arthington 2002). Environmental flows are regulated flow  
63 releases from a reservoir specifically for environmental benefits and are now widely used to help  
64 manage riverine environments and mitigate the impacts of flow regulation (Arthington et al. 2006).  
65 Environmental flows may benefit native riparian vegetation via the promotion of plant recruitment  
66 from soil seedbanks. However, that is dependent on the composition of the riparian soil seedbank,  
67 with a positive response reliant on an intact native seedbank and limited abundance of exotic  
68 species (Siebentritt et al. 2004; Richardson et al. 2015).

69 Soil seedbanks form when seed is deposited at a site and incorporated into the soil matrix. In  
70 riverine environments, this can happen through a range of vectors such as hydrochory (dispersal via  
71 water), wind, animals, human intervention and seed falling from extant vegetation. Hydrochory is  
72 likely to be most influential where flooding is frequent (Goodson et al. 2001, Leyer 2006) and of  
73 particular importance in regulated rivers where local propagule sources may be depauperate  
74 (Merritt et al. 2010). Furthermore, riparian or flood tolerant plant species often have propagules  
75 adapted to dispersal by water and thus are likely to favoured in sites where hydrochory is the  
76 primary dispersal vector (Nilsson et al. 2010; Soons et al. 2017).

77 Riparian seedbanks do not form uniformly, and their composition may vary with channel  
78 geomorphology as sediments (and propagules) are deposited by flows differently along a river (Fryirs  
79 and Brierley, 2001). Bars, benches and floodplains are three commonly identified riverine  
80 geomorphic features. Bars are in-stream features that are raised above the riverbed and can be  
81 attached to the bank or within the stream (Fryirs and Brierley, 2001). Benches are flat features

82 attached to the bank between the riverbed and the floodplain (Vietz et al. 2004). Bars are formed  
83 predominantly by the lateral accretion of bedload sediments, and so often form in zones with more  
84 vigorous hydraulic conditions, whereas, benches are formed predominantly by vertical deposition of  
85 fine-grained, suspended sediment and as such are more hydraulically conducive zones for deposition  
86 (Vietz et al. 2004). Both bars and benches are classified as 'in-channel' features, unlike floodplains  
87 that occur beyond and adjacent to the channel (Kemp 2004). While the contrasting fluvial processes  
88 that form these geomorphic features could be expected to lead to divergent soil seed bank  
89 composition, such differences have not been consistently observed (e.g. Gurnell et al. 2007;  
90 O'Donnell et al. 2015).

91 The dynamic nature of river flows means that riparian soil seedbanks are particularly important for  
92 river ecosystem health with stored seed enabling vegetation to rapidly recover after a disturbance  
93 event such as flooding (Reid and Capon 2011; O'Donnell et al. 2014). However, riparian soil  
94 seedbanks tend to mainly consist of early stage colonisers such as rushes and sedges, with lower  
95 abundances of other types of plants (e.g. woody plants) potentially limiting their usefulness as a tool  
96 for restoration where the seedbank does not match the extant or desired plant composition  
97 (Thompson and Grime, 1979; Lu et al. 2010; Greet 2016). A predominance of exotic species may  
98 even mean soil seedbanks act as a hindrance to restoration, and this may be particularly likely along  
99 degraded rivers in agricultural landscapes (Williams et al. 2008; O'Donnell et al. 2015; Dalton et al.  
100 2017). Conversely, where flooding is more frequent, flood tolerant (riparian and other flood tolerant  
101 species) and native species may be favoured (Catford and Downes 2010; Stokes et al. 2010; Catford  
102 et al. 2011) and thus the suitability of the seedbank for restoration purposes is greater.

103 Significant environmental management investment has occurred within Australia's largest and most  
104 altered river basin, the Murray Darling Basin (Kingsford 2000). With much of this landscape cleared  
105 for agriculture, widespread efforts at various governmental levels are being made to improve the  
106 condition and function of riparian zones within the Basin, primarily through environmental flows.

107 Environmental flow managers consider the inundation of benches a key target (Vietz et al. 2004), but  
108 the effectiveness of this for restoring native riparian vegetation is not well understood. More  
109 generally, the suitability of riparian seedbanks for restoration, as well as variation in soil seedbank  
110 composition across geomorphic features is uncertain and requires further investigation (Boudell and  
111 Stromberg 2010; O'Donnell 2014; Lu et al. 2010; Dawson 2017a).

112 This study was conducted as part of the Victorian Environmental Flows Monitoring and Assessment  
113 Program (VEFMAP) with the aim to provide information to help improve environmental flow  
114 management. Our study was conducted on the Campaspe River, part of the southern Murray-Darling  
115 Basin, as a case study of a highly regulated river within a cleared agricultural landscape. Specifically,  
116 we aimed to investigate patterns in soil seedbank composition associated with gradients in flooding  
117 frequency represented by different geomorphic features (bars, benches and floodplains), from  
118 frequently flooded (bars), to infrequently flooded (floodplain). We tested the following hypotheses:  
119 1) soil seedbank composition differs between geomorphic features; and there is a higher prevalence  
120 of 2) flood tolerant (riparian and other flood tolerant species), and 3) native species, in the soil  
121 seedbanks of in-channel features (bars and benches) compared to floodplains.

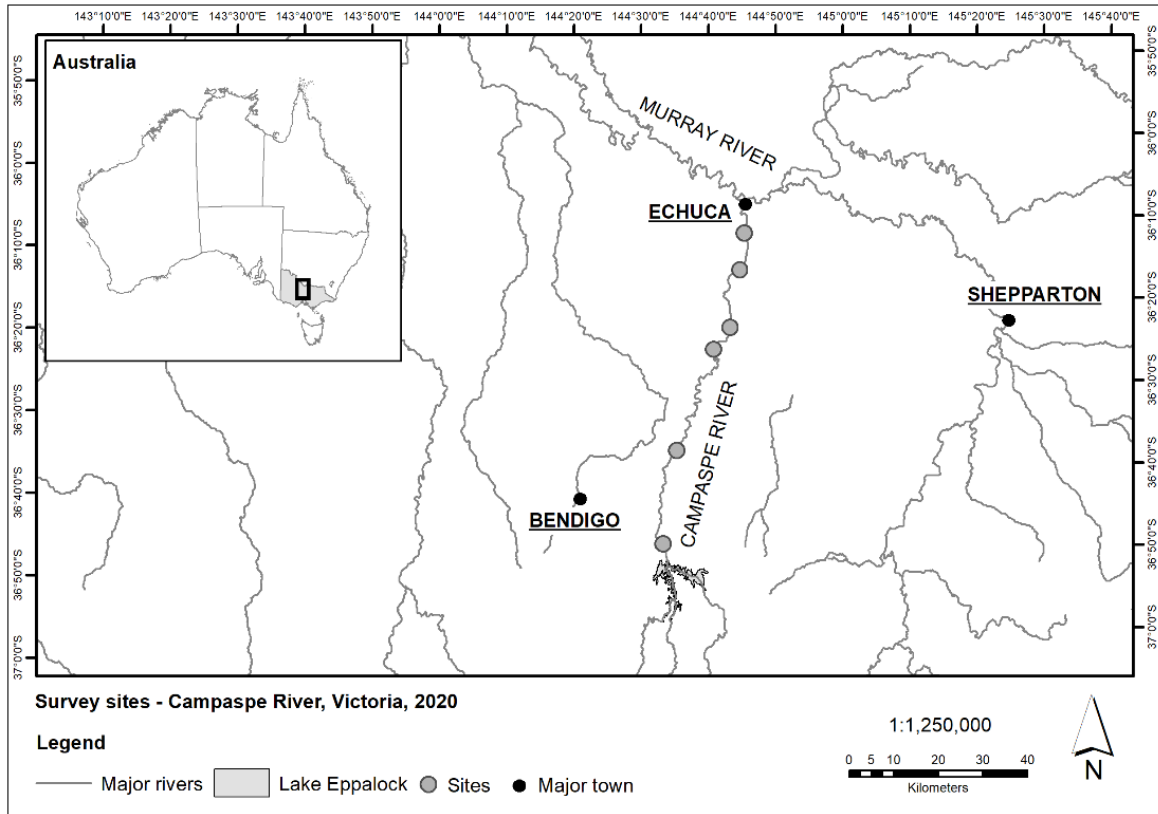
122

## 123 **Methods**

### 124 **Study sites**

125 Our study was conducted along the Campaspe River, Victoria, Australia, which is part of the Murray-  
126 Darling Basin, and heavily regulated for agricultural purposes. Catchment inflows are stored in Lake  
127 Eppalock, a large reservoir, where flows are managed and released for consumptive and  
128 environmental purposes. Mean annual rainfall and mean maximum temperatures (from 2010 to  
129 2020) varies along the length of the river from: rainfall = 541 mm and temp. = 21.8°C (Bendigo  
130 Airport, upstream) to rainfall = 414 mm and temp. = 23.4°C (Echuca, downstream) (Bureau of  
131 Meteorology 2020). The river frontages are publicly accessible Crown land, with restrictions on  
132 public use, but there is extensive adjacent land clearing and livestock grazing along the system,  
133 including licenced grazing of approximately 25% of the river frontage (Darren White, pers. com.).

134 The dominant vegetation type of the study area is floodplain riparian woodland, characterised by  
135 large River Red Gums (*Eucalyptus camaldulensis*) with a low cover of other woody species (e.g.  
136 *Callistemon* and *Acacia* spp.) and an understorey dominated by graminoids. The extant understorey  
137 vegetation of the river's floodplains is dominated by exotic species, mainly pasture grasses and  
138 exotic terrestrial herbs. The extant understorey vegetation composition within the channel is varied,  
139 with a mixture of native and exotic grasses, herbs, rushes and sedges, with wetter areas more  
140 commonly dominated by sedges (e.g. *Cyperus eragrostis* and *Cyperus exaltatus*), rushes (e.g. *Juncus*  
141 *amabilis*) and herbs (e.g. *Persicaria* spp.), and dryer areas are dominated by grass species such as  
142 *Lachnagrostis filiformis* and *Poa labillardierei*. The tree canopy along the river is narrow (typically 10-  
143 50 m wide) due to clearing of the broader landscape for agriculture, and shrub cover is sparse. Soil  
144 seedbank sampling was conducted at six long-term VEFMAP monitoring sites along the Campaspe  
145 River, between Lake Eppalock and Echuca. The GPS coordinates for each site are provided in  
146 Supplementary Material, Table S1.



147

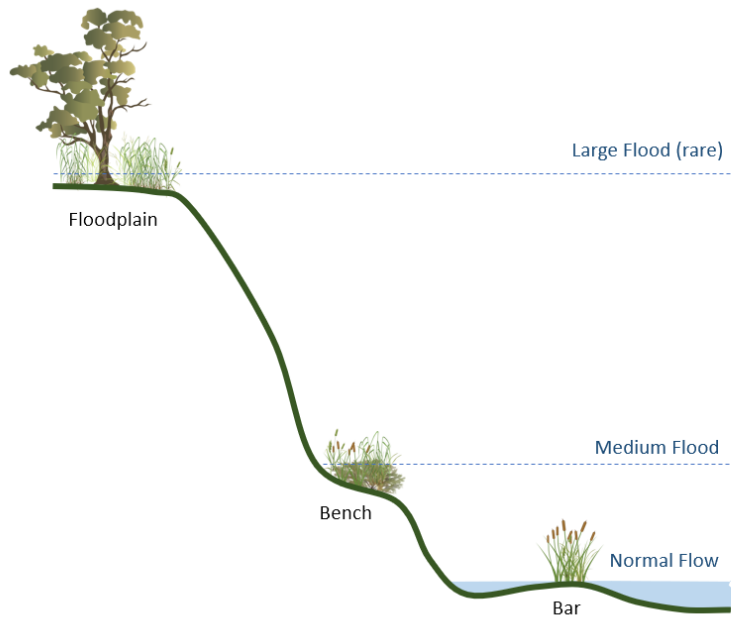
148

**Fig 1 Map of the Campaspe River, Victoria, Australia, with the six sampling sites indicated.**

149 **Study design**

150 Three riverbank geomorphic features were sampled—bars, benches and floodplains. These  
151 represent a gradient in elevation, and thus flooding frequency. Bars included mid-channel and point  
152 bars (adjacent to the bank) and are flooded most often as they are at the lowest elevation. Benches  
153 are depositional features along the bank within the channel, and are flooded intermittently, while  
154 the floodplain is outside of the channel and only inundated by large floods (Fig 2).

155 Soil seedbank sampling was conducted on the 21<sup>st</sup> and 22<sup>nd</sup> of February 2019 in dry conditions. This  
156 was before the release of a small environmental flow by water authorities. Timing sample collection  
157 in this manner meant that low elevation features, namely bars, could be accessed. At each of the  
158 study sites, an appropriate bar, bench and floodplain was selected according to the following  
159 criteria. Firstly, each of the features had to be relatively flat and sufficiently large enough to fit a 2m  
160 x 2m quadrat. Bars had to be adjacent to the water's edge on at least one side. Benches selected  
161 were approximately 1m higher in elevation than the bars, as this bench elevation was common at all  
162 sites. Appropriate floodplain locations were selected adjacent to the channel. The difference in  
163 elevation between the bench and the floodplain was less consistent but ranged from 4–7m.



164

165 **Fig 2 Cross-sectional schematic diagram of the river channel with three geomorphic features where soil**  
 166 **seedbank sampling was done indicated. Sampled benches were approximately 1m higher than sampled**  
 167 **bars, and sampled floodplains were approximately 4–7m above benches. Plant images courtesy of the**  
 168 **Integration and Application Network, University of Maryland Center for Environmental Science**  
 169 **(ian.umces.edu/imagelibrary/)**

170

171 **Soil seedbank sample collection and processing**

172 At each feature within a site, a 2m x 2m quadrat was haphazardly placed. One soil sample was  
 173 collected from each corner and one from the centre of each quadrat (five in total per feature), a  
 174 sampling design adapted from that used by Lunt (1997). Surface debris such as fallen leaves and  
 175 twigs was cleared prior to sampling. All soil samples were 5 x 5 x 5cm (5cm<sup>3</sup>) in volume. In total, 15  
 176 samples were collected from each of the six sites over two days, giving a total of 90 soil samples  
 177 overall. Samples were placed in labelled plastic bags and stored in a darkened insulated container.

178 Samples were taken to the Burnley Campus of The University of Melbourne on 22<sup>nd</sup> February. There,  
 179 samples were transferred into foil trays and dried in an oven at 30°C for one week. Drying has been  
 180 shown to enhance the germination of many Australian wetland species, as well as being an effective  
 181 trigger for many of the terrestrial invaders of riparian systems (Brock and Casanova 2000). After  
 182 drying, a pestle was used to gently break up any large clods in a mortar and the soil was sifted to

183 remove large leaves or other debris larger than half a centimetre. Each sample was then spread over  
184 seed raising mix in 30cm x 20cm x 4cm seedling trays and watered until saturated. The ninety trays  
185 were then placed in random positions within a temperature-controlled glasshouse, with  
186 temperatures maintained between 15°C and 25°C, which are common glasshouse temperatures for  
187 seed germination and correspond with mean annual maximum temperatures of the study area. Six  
188 controls of only seed raising mix were also placed in the glasshouse to monitor for contamination  
189 (none was observed). Samples were automatically watered by a sprinkler system three times a day  
190 for ten minutes at a time, which kept them moist. All trays were fertilized every four weeks using a  
191 0.5g/20L concentration of Peters® Professional fertiliser (N:P:K = 20:8.7:16.6).

192 Once seedlings were identified to species (where possible) or genus level, they were removed,  
193 tallied and discarded. Seedlings that were difficult to identify were potted up to facilitate  
194 accelerated growth and identification, in most cases. Samples were discarded once all visible  
195 seedlings were removed. All samples were discarded by the 10<sup>th</sup> of May 2019, after a period of 71  
196 days.

197

## 198 **Data analysis**

199 For all identified taxa, their origin (native or exotic) and flood tolerance were determined based on  
200 the scientific literature (Brock and Casanova 2000; Casanova 2011; Bull 2014; Richardson et al. 2016;  
201 Kew RBG 2019; Royal Botanic Gardens Victoria 2019). Seedling taxa were assigned to a binary  
202 category of flood tolerant or not, which largely correlated with the accepted definitions of  
203 riparian/wetland species or terrestrial species (full species list and assignments provided in  
204 Supplementary Material; Table S2). Flood tolerant species therefore included riparian (including  
205 aquatic and emergent) species as well as those that are tolerant to regular inundation associated  
206 with waterways. Definitions were made using multiple sources as there was no formalised set of  
207 riparian species groupings in Victoria. These sources included the Wetland Plant Functional Groups

208 (WPFPG, sensu Brock and Casanova 1997), Flora of Victoria website (Royal Botanic Gardens Victoria  
209 (2019) and known distributions or affiliations of plants to waterways. For each sample, we totalled  
210 the seedling abundances of each taxon, and taxa richness and seedling abundances for each sample  
211 for groupings based on plant origin and flood tolerance.

212 All statistical analyses were conducted using R version 3.6.0 (R, 2019). Firstly, to assess species  
213 composition differences between geomorphic features, we created a similarity matrix using the  
214 metaMDS function, and tested for differences using the envfit function, using the *vegan* package  
215 (Oksanen et al. 2013). Additionally, we used the *indicspecies* package (Cáceres and Legendre 2009)  
216 to determine species associations with different geomorphic features. Secondly, we used the *lme4*  
217 package (Bates et al. 2014) to build linear mixed-effects models to assess for differences in seed  
218 abundance and taxa richness between geomorphic features (fixed effect of feature only), and  
219 between geomorphic features in combination with plant origin or flood tolerance (fixed effects of  
220 feature and tolerance or origin, and their interaction). Site was included as a random factor in all  
221 models. Tukey's tests were used via the *emmeans* package (Lenth 2019) to test for differences  
222 between means when fixed effects were significant. Combined boxplots and scatterplots are  
223 presented to illustrate the data, and we report predicted means (rounded to whole numbers) for  
224 comparisons between group means. All data and code used in analyses are freely available here:  
225 <https://osf.io/4vaew/>.

226

227 **Results**

228 A total of 6515 seedlings were identified from the seedbank samples collected for this study, across  
 229 all features and sites. These comprised 55 different taxa, 27 of which were native, and 28 exotic. Of  
 230 the native taxa, 16 were flood tolerant and 11 flood intolerant. The opposite trend was found for  
 231 exotic species, only 7 exotic taxa were flood tolerant and 21 flood intolerant. 46 of the 55 seedbank  
 232 taxa were present in the extant vegetation in at least one site, and all of the most abundant species  
 233 within the seedbank were also present in the extant vegetation at all sites. A summary of the  
 234 numbers and types of taxa are listed in Table 1, and a full species list and their record within the  
 235 extant vegetation is provided in Supplementary Material; Table S2.

236 Monocots were the most abundant taxa present in the seedbank samples. Tall native perennial  
 237 rushes, grouped as *Juncus* spp. due to their phenotypical similarity, accounted for 58% of all  
 238 seedlings. This taxon consisted of both *Juncus amabilis* and *Juncus usitatus*, both of which have been  
 239 commonly recorded in the extant vegetation (Tonkin et al. 2020). Two sedge taxa, *Carex* spp. and  
 240 *Cyperus eragrostis*\* (asterisks used to identify exotic species), were also notably abundant (6% and  
 241 9% respectively), as were grasses such as the native flood tolerant *Lachnagrostis filiformis* (9%). Very  
 242 few tree or shrub seedlings were recorded (Table 1).

243 **Table 1. Summary of the growth form, origin, flood tolerance and seedling abundances of seedbank taxa.**

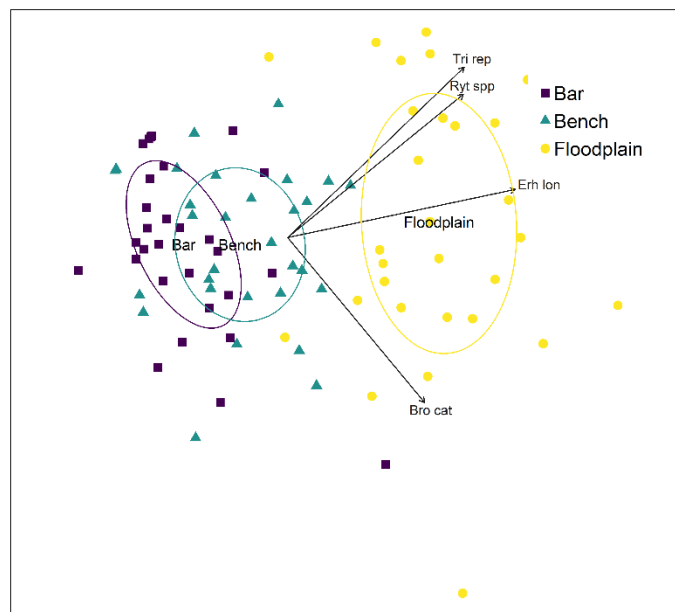
Growth form	No. of taxa	Origin		Flood tolerance		Total abundance of seedlings
		<i>Native</i>	<i>Exotic</i>	<i>Tolerant</i>	<i>Intolerant</i>	
Grass	11	4	7	4	7	1003
Sedge	3	1	2	3	0	1082
Rush	2	2	0	2	0	3840
Forb	37	18	19	12	25	579
Shrub	1	1	0	1	0	1
Tree	1	1	0	1	0	10
<b>Total</b>	<b>55</b>	<b>27</b>	<b>28</b>	<b>23</b>	<b>32</b>	<b>6515</b>

244

245 **Soil seedbank composition by feature**

246 The composition of the soil seedbank samples differed clearly by geomorphic feature ( $p < 0.001$ ), but  
247 not by site ( $p = 0.078$ ). Soil seedbank samples from bar and bench features were more similar to  
248 each other than to floodplain samples, which were least similar to bar samples (Figure 3).

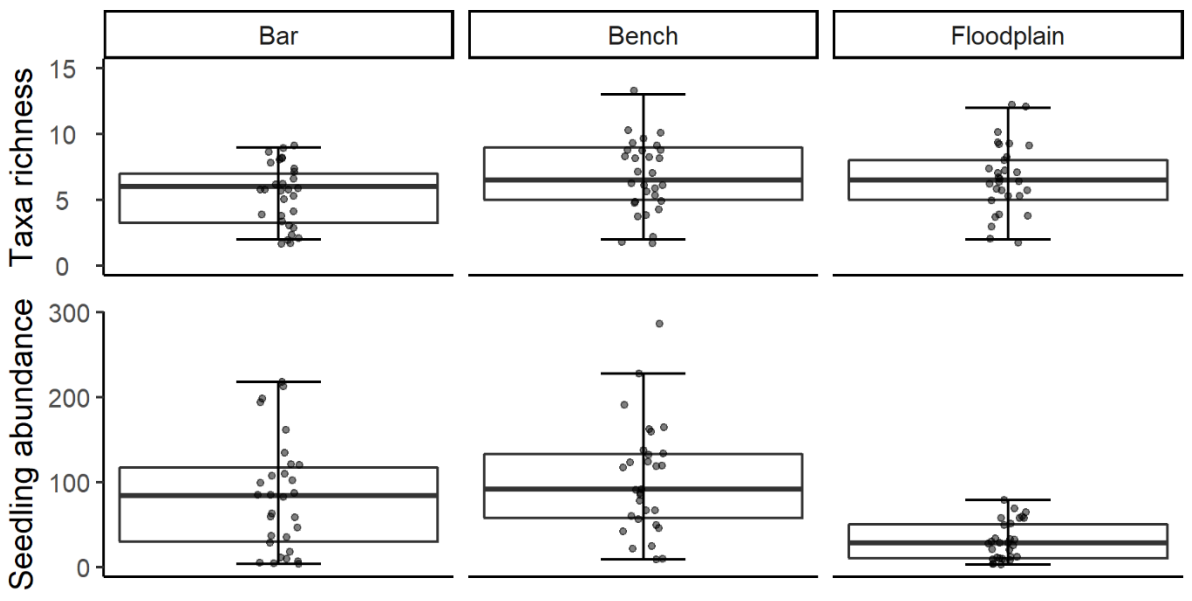
249 The species best associated with the ordination, *Bromus cartharticus*\*, *Rytidosperma* spp., *Trifolium*  
250 *repens*\* and *Ehrharta longiflora*\*, are all flood intolerant and were more common within floodplain  
251 samples. Indicator species analyses identified the native sedges *Carex* spp., and native flood tolerant  
252 forbs *Persicaria hydropiper* and *Persicaria prostrata* to be best associated with bar samples, and the  
253 native flood tolerant grass *Lachnagrostis filiformis* to be best associated with bench samples.



254  
255 **Fig 3 NMDS plot of soil seedbank composition by geomorphic feature. Feature labels indicate centroid of**  
256 **samples by feature. Species correlated best ( $p < 0.001$  and  $r^2 > 0.2$ ) with the ordination are shown. Species**  
257 **codes: Bro cat – *Bromus cartharticus*\*; Ryt spp – *Rytidosperma* spp.; Tri rep – *Trifolium repens*\*; Erh lon –**  
258 ***Ehrharta longiflora*\*.**

260 There was no clear evidence of a difference in overall taxa richness of the soil seedbanks between  
261 the different geomorphic features ( $p = 0.086$ ). A mean of  $5 \pm 1$  (mean  $\pm$  SE) taxa was recorded for bar  
262 samples,  $7 \pm 1$  for bench samples, and  $6 \pm 1$  for floodplain samples (Fig 4). Seedling abundances of  
263 the soil seedbank samples differed between geomorphic features ( $p < 0.001$ ), with highest  
264 abundances recorded for bench samples ( $91 \pm 20$  seedlings), intermediate abundances for bar  
265 samples ( $74 \pm 17$  seedlings) and lowest abundances for floodplain samples ( $27 \pm 6$  seedlings) (Fig 4).

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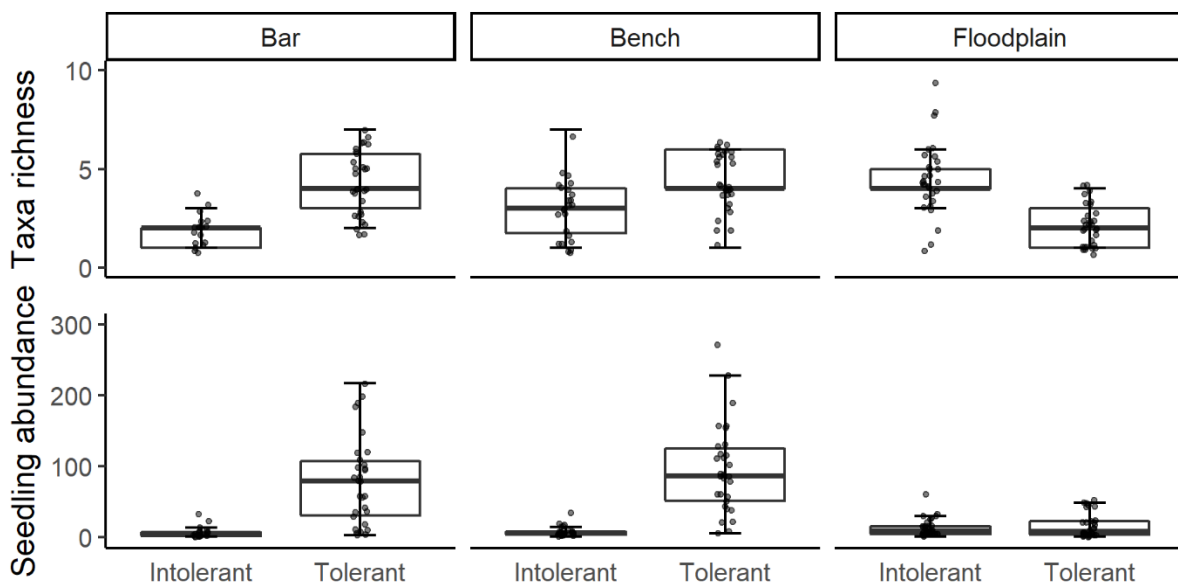
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**Fig 4** Boxplots of taxa richness (top) and seedling abundance (bottom) per sample for each of the three geomorphic features (pooling across all sites). Bolded lines represent median values, boxes comprise the interquartile range (IQR: 25<sup>th</sup> to 75<sup>th</sup> percentiles) and whiskers comprise all data within 1.5 × IQR from the 25<sup>th</sup> to 75<sup>th</sup> percentiles. Grey circles present raw data.

273 **Soil seedbank composition by feature and flood tolerance**

274 There were differences in flood tolerant and flood intolerant taxa richness by geomorphic feature  
275 (i.e. there was a significant interaction effect of feature and tolerance;  $p < 0.001$ ). More flood  
276 tolerant than flood intolerant taxa were recorded for bar samples,  $4 \pm 1$  cf.  $2 \pm 0$ . Similar numbers of  
277 flood tolerant and flood intolerant taxa were recorded for bench samples,  $4 \pm 1$  cf.  $3 \pm 0$ . Conversely,  
278 floodplain samples contained fewer flood tolerant taxa than flood intolerant taxa:  $2 \pm 0$  cf.  $4 \pm 1$   
279 (Figure 5).

280 There were greater abundances of flood tolerant than flood intolerant seedlings overall ( $p < 0.001$ ;  
281 Figure 5). There were also differences in the abundances of seedlings of flood tolerant and flood  
282 intolerant by feature (i.e. there was a significant interaction between feature and tolerance;  $p$   
283  $< 0.001$ ). Much greater abundances of flood tolerant than flood intolerant seedlings were recorded  
284 for bar ( $70 \pm 15$  cf.  $5 \pm 1$ ) and bench ( $85 \pm 19$  cf.  $5 \pm 2$ ) samples, while abundances for floodplain  
285 samples were similar ( $15 \pm 3$  cf.  $13 \pm 3$ ).



286  
287 **Fig 5** Boxplots of flood tolerant and flood intolerant taxa richness (top) and seedling abundance (bottom)  
288 per sample for each of the three geomorphic features (pooling across all sites). Bolded lines represent  
289 median values, boxes comprise the interquartile range (IQR: 25<sup>th</sup> to 75<sup>th</sup> percentiles) and whiskers comprise  
290 all data within  $1.5 \times$  IQR from the 25<sup>th</sup> to 75<sup>th</sup> percentiles. Grey circles present raw data.

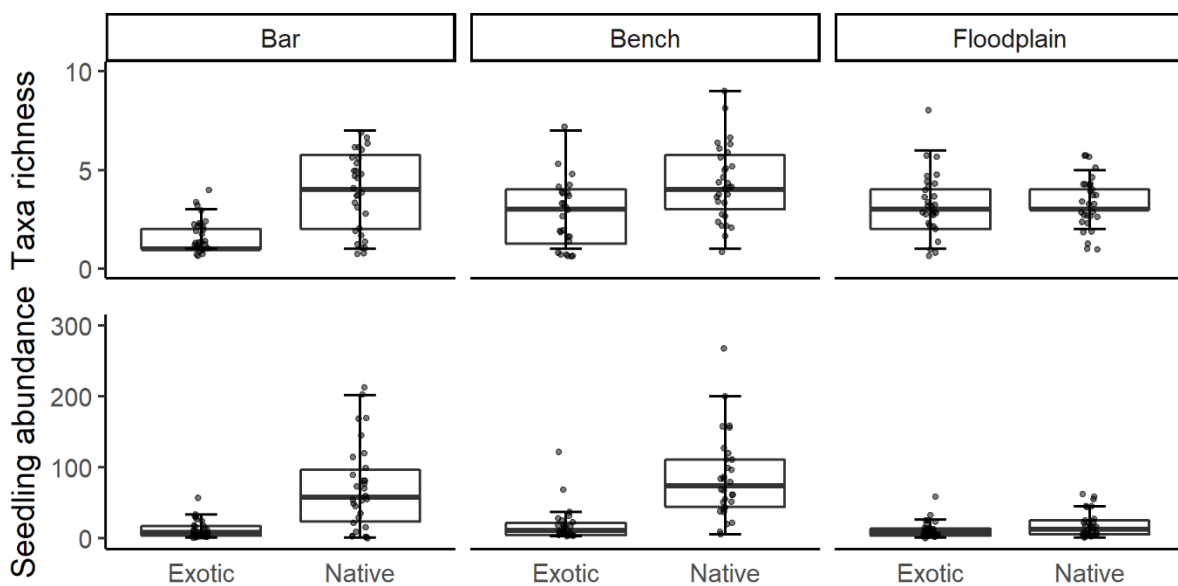
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292

293 **Soil seedbank composition by feature and origin**

294 Greater richness of native than exotic taxa was recorded for the seedbank samples overall (p  
295 <0.001). There were also differences in native and exotic taxa richness by geomorphic feature (i.e.  
296 there was a significant interaction effect of feature and origin; p <0.001). Native taxa richness was  
297 greater than exotic taxa richness for bar ( $4 \pm 1$  cf.  $2 \pm 0$ ) and bench ( $4 \pm 1$  cf.  $3 \pm 0$ ) samples. In  
298 contrast, native and exotic taxa richness for floodplain samples were similar:  $3 \pm 0$  for both (Fig 6).

299 Much greater abundances of native than exotic seedlings were identified from the seedbank  
300 samples overall (p <0.001). There were also differences in the abundances of seedlings of native and  
301 exotic taxa by feature (i.e. there was a significant interaction effect; p <0.001). Native seedling  
302 abundances were greater than exotic seedling abundances for all features, but these differences  
303 were much greater for in channel features: bars ( $63 \pm 14$  cf.  $11 \pm 3$ ) and benches ( $76 \pm 17$  cf.  $17 \pm 4$ ),  
304 than floodplains ( $17 \pm 4$  cf.  $11 \pm 2$ ) (Figure 6).



305

306 **Fig 6** Boxplots of native and exotic taxa richness (top) and seedling abundance (bottom) per sample for each  
307 of the three geomorphic features (pooling across all sites). Bolded lines represent median values, boxes  
308 comprise the interquartile range (IQR: 25<sup>th</sup> to 75<sup>th</sup> percentiles) and whiskers comprise all data within 1.5 ×  
309 IQR from the 25<sup>th</sup> to 75<sup>th</sup> percentiles. Grey circles present raw data.

310

## 311 **Discussion**

312 We found clear patterns in soil seedbank composition associated with different river channel  
313 features. Overall, the composition of soil seedbanks of in-channel features (bars and benches) were  
314 much more similar to each other than soil seedbanks of the adjacent floodplain. Seed abundances in  
315 the soil seedbank of in channel features were higher than that of floodplains, but there was no  
316 corresponding difference in the taxa richness. Soil seedbanks of in-channel features were dominated  
317 by flood tolerant and native taxa, whereas floodplain seedbanks were associated with flood  
318 intolerant and exotic taxa. All of the most abundant species within the seedbank were flood tolerant  
319 plant species that were present in the extant vegetation at all sites. Given such patterns, we suggest  
320 that environmental flows which regularly inundate in-channel features, particularly those that mimic  
321 natural flow patterns, will promote the maintenance of native riparian plant communities where  
322 there are few exotic flood tolerant species present within the extant vegetation.

### 323 *Patterns of soil seedbank composition in relation to different geomorphic features*

324 Our results are consistent with other studies which have found variation in soil seedbank  
325 composition in association with geomorphic gradients (Abernethy and Willby 1999; Holzel and Otte  
326 2001; Capon and Brock 2006; Leyer 2006; Capon 2007; James et al. 2007; Dawson 2017b, 2020). Like  
327 many of these studies, we found that more frequently flooded geomorphic features had more  
328 abundant soil seedbanks than those less frequently flooded (e.g. Holzel and Otte 2001; Capon 2007;  
329 Dawson et al. 2017b). Similarly, we found that while the species richness of the soil seedbank across  
330 these geomorphic gradients were similar, species-level patterns differed, with frequently flooded  
331 sites dominated by highly abundant annuals and small-seeded monocots (particularly sedges and  
332 rushes), while perennial grasses were more common at infrequently flooded sites (Abernethy and  
333 Willby 1999; Capon and Brock 2006; O'Donnell 2014).

334 However, our results contrast with those of O'Donnell et al. (2013, 2014) who found the seedbank  
335 composition of the same three features we studied (bars, benches and floodplain) to be more

336 similar. They reported the propagule abundance of soil seedbanks of bars to be highly variable and  
337 to have lower taxa richness than benches or floodplains. They suggested this reflected the relatively  
338 frequent disturbances experienced by bars with flows not only depositing seed, but also scouring  
339 and eroding the soil seedbank—bars are features that are considered transient, and subject to  
340 frequent erosion as well as deposition (Fryirs and Brierley 2001; O’Donnell et al. 2014). Bars which  
341 we sampled are probably less transient due to the heavily regulated nature of our study system.  
342 Nonetheless, in both our study and theirs, the propagules within the soil seedbank of benches were  
343 found to be more abundant and species-rich than bars, likely reflecting their nature as depositional  
344 features less subject to erosion than bars.

345 *Soil seedbanks of in-channel features contain more riparian and fewer terrestrial species than*  
346 *floodplains*

347 More flood tolerant taxa were found within the soil seed banks of in-channel features than  
348 floodplains, as predicted. Our results are consistent with other studies that have found the soil seed  
349 banks of more frequently inundated geomorphic features to contain higher numbers and propagule  
350 abundances of riparian plant species (Dawson et al. 2017b, 2020). Frequently inundated geomorphic  
351 features such as in-channel benches and bars are likely to accumulate seeds from deposition  
352 following flow events. Many riparian plants produce propagules that are well adapted to disperse via  
353 water (hydrochory) and are thus likely to be preferentially deposited in regularly flooded sites  
354 (Dawson 2017c; Soons et al. 2017).

355 Our study system, the Campaspe River, is heavily regulated and thus the floodplain now rarely  
356 floods. Infrequently flooded floodplain seedbanks are more likely to reflect what would be found in  
357 terrestrial environments; however, some floodplain seedbanks have been shown to also contain  
358 comparable numbers of riparian plants species as in-channel features (O’Donnell 2013). The lower  
359 taxa richness and seed abundances of riparian plant species found in our floodplain samples may be  
360 a result of their agricultural legacy, which has been demonstrated to adversely affect riparian plant

361 soil seed banks (Casanova 2012; Dawson 2017a, 2020). Additionally, cultivation is likely to promote  
362 the predominance of terrestrial species in the soil seed bank, such as we observed (Dawson 2017a).

### 363 *Soil seedbanks of in-channel features contain more native species than floodplains*

364 Within riparian zones of the Murray-Darling Basin, where our study was undertaken, the majority of  
365 exotic species are terrestrial species (Catford et al. 2014). Conversely, most flood tolerant riparian  
366 species are native (although native terrestrial species are also common). Therefore, within the  
367 region, flow regulation resulting from damming and water extraction for agriculture and thus a  
368 general drying of conditions in riverine environments has favoured exotic species and caused a  
369 decline in native riparian species (Catford and Downes 2010; Stokes et al. 2010; Catford et al. 2011).  
370 It is thus unsurprising that the pattern we observed for native/exotic taxa mirrored that for flood  
371 tolerant/intolerant plants—native taxa predominated in the soil seedbank of in-channel features.

372 Our results are consistent with studies by Dawson et al. (2017b, 2020) with greater abundances of  
373 native species found in more frequently inundated areas. Conversely, exotic species were generally  
374 associated with areas of less frequent flooding and more intense agricultural land use (Dawson et al.  
375 2017b), floodplains in our case. Indeed, increases in the proportion of non-native species in soil seed  
376 banks with increasing agricultural intensity have been commonly reported (Eldridge and Lunt 2010;  
377 O'Donnell et al. 2015; Dalton 2017; Dawson 2017a, 2017b). However, while we found many exotic  
378 species, particularly pasture grasses such as *Bromus catharticus*\*, were associated with areas of  
379 infrequent flooding (floodplains), we found exotic seedling abundances were higher in the soil  
380 seedbanks of benches than floodplains. This may reflect the combined contributions of hydrochoric  
381 seed deposition of the abundant flood tolerant exotic rush, *Cyperus eragrostis*\*, as well as seed  
382 inputs from local extant terrestrial vegetation via wind dispersal during the prolonged periods  
383 without flooding within our regulated study system, that are also common throughout the Murray-  
384 Darling Basin.

### 385 *Implications for environmental flow management*

386 Increasingly, river restoration in Australia and globally relies on the reinstatement or mimicking of  
387 natural flow regimes to restore vegetation communities (Poff et al. 1997; Arthington and Pusey  
388 2003). The resilience of native riparian vegetation and its prospects for a positive response to  
389 environmental flows are in part dependent of the presence of a native riparian soil seedbank  
390 (Siebentritt 2004; Boudell and Stromberg 2008; Dawson 2017a). Our study identified such conditions  
391 and may suggest that both: soil seedbanks are contributing to the fact that environmental flows are  
392 already achieving positive results in the Campaspe River (Tonkin et al. 2020); and that there is  
393 potential for greater benefit. An increase in depth and frequency of environmental flow releases  
394 may further promote native riparian vegetation within the channel in cases where the riparian soil  
395 seedbank is dominated by native flood tolerant species, such as the Campaspe River. Conversely, the  
396 majority of exotic taxa identified in this study were flood intolerant and increases in environmental  
397 flows may also decrease the extent of such species and, ideally, confine them to the upper bank and  
398 floodplain (Miller et al. 2013), where environmental flows do not reach.

399 While there were similar numbers of native than exotic taxa in the soil seedbank overall, the  
400 abundance of native propagules, particularly for in-channel features, was much greater. This was in  
401 part due to the dominance of native rushes (*Juncus* spp.) in the soil seedbank that are also common  
402 in the extant vegetation throughout the river. This is a positive finding, as flood tolerant rushes have  
403 the ability to stabilise the sediments of bars and benches by reducing the velocity of flowing water  
404 (O'Donnell et al. 2015) and would be likely to recruit abundantly from the soil seedbank following  
405 environmental flows. While the suitability of riparian seedbanks for restoration is sometimes  
406 uncertain (Siebentritt 2004; Boudell and Stromberg, 2008; Lu et al., 2010), our study provides  
407 evidence that they can be an important source of propagules for the recruitment of native  
408 herbaceous vegetation.

409 There are many other factors that can influence the composition of riparian soil seedbanks that we  
410 did not explore such as seed size and longevity. Seed size and shape can influence dispersal and

411 deposition patterns and how easily a seed is buried, with rounded smaller seeds more easily buried  
412 (O'Donnell et al. 2013; Dawson 2020;). For example, *Juncus* species have very small seeds that are  
413 produced in high abundances which is likely to have contributed to their abundance in the soil  
414 seedbank in our study. Seed longevity obviously affects persistence in the seedbank (Thompson et  
415 al. 1993), with some species such as the dominant tree in our study system, the river red gum  
416 (*Eucalyptus camaldulensis*), producing short-lived seeds not typically represented in the soil  
417 seedbank (Greet 2013). For such species, environmental flow timing and sequencing may be critical  
418 to their recruitment (Greet 2012). Given the shallow seedbank samples within regularly inundated  
419 features, recent high rainfall events on the floodplain, and the seedbank composition, the seedbank  
420 was likely reflective of recent propagule deposition or dispersal rather than long-lived seed from  
421 much older deposition events.

422 As well as flow magnitude and timing it is also important to consider water availability when  
423 planning environmental flows (Tonkin et al. 2020). This is particularly important in water-scarce  
424 regions such as the Murray-Darling region due to competing demands for water, with greater  
425 allocations of water to environmental flows potentially having important economic and social  
426 implications (Wei et al. 2011). Lastly, we acknowledge that propagule germination is dependent on  
427 many factors, such as dormancy and environmental triggers such as fire or moisture (Auld and  
428 O'Connell 1991; Baskin and Baskin 1998). It is likely that our germination assays did not meet the  
429 germination requirements of all species present within the soil seedbank samples collected (Gross  
430 1990; Nielsen et al. 2018). Nonetheless, we are confident that we were able to provide appropriate  
431 conditions for the germination for the vast majority of propagules in the collected samples (Poiani  
432 and Johnson 1988; Gurnell et al., 2007; Dawson et al. 2017a).

433

434 **Conclusion**

435 We found that propagules of native flood tolerant taxa dominated the seedbanks of in-channel  
436 features of a heavily regulated river subject to environmental flows. Conversely, exotic pasture  
437 grasses and other terrestrial species were less common within the soil seedbank of in-channel  
438 features. Environmental flows are currently being used successfully to discourage the growth of  
439 terrestrial exotic species within the channel, and these may be helping to maintain some level of  
440 resilience of the riparian vegetation to flow disturbances through increasing the prevalence of  
441 inundation tolerant riparian species. Furthermore, strategic increases to the frequency, depth,  
442 duration and further consideration of the timing of flow releases may help to further encourage the  
443 establishment of native riparian vegetation.

444

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## 453 **References**

454

455 Abernethy, V. J. and N. J. Willby (1999) Changes along a disturbance gradient in the density and  
456 composition of propagule banks in floodplain aquatic habitats. *Plant Ecology* 140(2): 177-190.

457

458 Arthington, A.H., Bunn, S.E., Poff, N.L. and Naiman, R.J. (2006) The challenge of providing  
459 environmental flow rules to sustain river ecosystems. *Ecological applications* 16(4): 1311-1318.

460

461 Arthington, A. H. and Pusey, B. J. (2003) Flow restoration and protection in Australian rivers. *River*  
462 *research and application*, 19(5-6): 377-395.

463

464 Auld, T. D. and O'Connell, M. A. (1991) Predicting patterns of post-fire germination in 35 eastern  
465 Australian Fabaceae. *Australian Journal of Ecology*, 16(1): 53-70.

466

467 Baskin, C. C. and Baskin, J. M. (1998) *Seeds: ecology, biogeography, and evolution of dormancy and*  
468 *germination*. San Diego, CA, USA, Academic Press.

469

470 Bates, D., Mächler, M., Bolker, B. and Walker, S. (2014) Fitting linear mixed-effects models using  
471 lme4. *Journal of Statistical Software* 67(1): 1-48

472

473 Bureau of Meteorology (2020) *Climate data online*. <http://www.bom.gov.au/climate/data>  
474 Accessed 2 September 2020

475

476 Boudell J.A. and Stromberg J.C. (2008) Propagule banks: potential contribution to restoration of an  
477 impounded and dewatered riparian ecosystem. *Wetlands* 28, 656-665.

478

479 Brock, M. A. and Casanova, M. T. (1997) Plant life at the edges of wetlands; ecological responses to  
480 wetting and drying patterns. *Frontiers in Ecology: building the links*: 181-192

481

482 Brock, M. A. and Casanova, M. T. (2000) How do depth, duration and frequency of flooding influence  
483 the establishment of wetland plant communities? *Plant Ecology* 147(2): 237-250.

484

485 Bull, M. (2014) *Flora of Melbourne: A Guide to the Indigenous Plants of the Greater Melbourne Area*.  
486 Hyland House Publishing.

487

488 Bunn, S. E. and Arthington, A. H. (2002) Basic principles and ecological consequences of altered flow  
489 regimes for aquatic biodiversity. *Environmental Management* 30(4): 492-507.

490

491 Cáceres, M. D. and Legendre, P. (2009) Associations between species and groups of sites: indices and  
492 statistical inference. *Ecology* 90(12): 3566-3574.

493

494 Capon, S. J. (2007) Effects of flooding on seedling emergence from the soil seed bank of a large  
495 desert floodplain. *Wetlands* 27(4): 904-914.

496

497 Capon, S. J. and Brock, M. A. (2006) Flooding, soil seed bank dynamics and vegetation resilience of a  
498 hydrologically variable desert floodplain. *Freshwater Biology* 51(2): 206-223.

499

500 Casanova, M.T. (1997). Plant life at the edges of wetlands; ecological responses to wetting and  
501 drying patterns. In: *Frontiers in Ecology; Building the Links* 181– 192.

502 Casanova, M. T. (2011) Using water plant functional groups to investigate environmental water

503 requirements. *Freshwater Biology* 56: 2637-2652.  
504  
505  
506 Catford, J. A. and Downes, B. J. (2010) Using multi-scale species distribution data to infer drivers of  
507 biological invasion in riparian wetlands. *Diversity and Distributions* 16(1): 20-32.  
508  
509 Catford, J. A., Downes, B. J., Vesk, P. and Gippel, C. J. (2011) Flow regulation reduces native plant  
510 cover and facilitates exotic invasion in riparian wetlands. *Journal of Applied Ecology* 48(2): 432-442.  
511  
512 Catford, J. A., Morris, W. K., Vesk, P. A. Gippel, C. J., and Downes, B. J (2014) Species and  
513 environmental characteristics point to flow regulation and drought as drivers of riparian plant  
514 invasion. *Diversity and Distributions* 20(9): 1084-1096.  
515  
516 Dalton, R. L., Carpenter, D. J., Boutin, C. and Allison, J. E. (2017) Factors affecting soil seed banks of  
517 riparian communities in an agricultural ecosystem: potential for conservation of native plant  
518 diversity. *Applied Vegetation Science*, 20(3), 446-458.  
519  
520 Dawson, S. K., Catford, J. A., Berney, P., Kingsford, R. T. and Capon, S. (2020) Land use alters soil  
521 propagule banks of wetlands down the soil-depth profile. *Marine and Freshwater Research* 71(2):  
522 191-201.  
523  
524 Dawson, S. K., Kingsford, R. T., Berney, P., Catford, J. A., Keith, D. A., Stoklosa, J. and Hemmings, F.  
525 A. (2017a) Contrasting influences of inundation and land use on the rate of floodplain  
526 restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* 27(3): 663-674.  
527  
528 Dawson, S. K., Kingsford, R. T., Berney, P., Keith, D. A., Hemmings, F. A., Warton, D. I., Waters, C. and  
529 Catford, J. A. (2017b) Frequent inundation helps counteract land use impacts on wetland propagule  
530 banks. *Applied Vegetation Science* 20(3): 459-467.  
531  
532 Dawson, S. K., Warton, D. I., Kingsford, R. T., Berney, P., Keith, D. A. and Catford, J. A. (2017c) Plant  
533 traits of propagule banks and standing vegetation reveal flooding alleviates impacts of agriculture on  
534 wetland restoration. *Journal of Applied Ecology* 54(6): 1907-1918.  
535  
536 Eldridge, D. J. and Lunt, I. D. (2010) Resilience of soil seed banks to site degradation in intermittently  
537 flooded riverine woodlands. *Journal of Vegetation Science* 21(1): 157-166.  
538  
539 Fryirs, K. and Brierley, G.J. (2001) Variability in sediment delivery and storage along river courses in  
540 Bega catchment, NSW, Australia: implications for geomorphic river recovery. *Geomorphology* 38(3-  
541 4): 237-265.  
542  
543 Goodson, J. M., Gurnell, A., Angold, P. G. and Morrissey, I. P. (2001) Riparian seed banks: structure,  
544 process and implications for riparian management. *Progress in Physical Geography* 25(3): 301-325.  
545  
546 Greet, J. (2016) The potential of soil seed banks of a eucalypt wetland forest to aid restoration.  
547 *Wetlands Ecology and Management* 24(5): 1-13.  
548  
549 Greet, J., Cousens, R. and Webb, J. A. (2012) Flow regulation affects temporal patterns of riverine  
550 plant seed dispersal: potential implications for plant recruitment. *Freshwater Biology* 57(12): 2568-  
551 2579.  
552  
553 Greet, J., Cousens, R. and Webb, J. A. (2013) Flow regulation is associated with riverine soil seed

554 bank composition within an agricultural landscape: potential implications for restoration. *Journal of*  
555 *Vegetation Science* 24(1): 157-167.

556

557 Grill, G., et al. (2019) Mapping the world's free-flowing rivers. *Nature* 569(7755): 215-221.

558

559 Gross, K. L. (1990) A comparison of methods for estimating seed numbers in the soil. *Journal of*  
560 *Ecology* 78(4): 1079-1093.

561

562 Gurnell, A., Goodson J., Thompson K., Mountford O. and Clifford N. (2007) Three seedling emergence  
563 methods in soil seed bank studies: implications for interpretation of propagule deposition in riparian  
564 zones. *Seed Science Research* 17(3): 183-199

565

566 Holzel, N. and Otte, A. (2001) The impact of flooding regime on the soil seed bank of flood-meadows.  
567 *Journal of Vegetation Science* 12(2): 209-218.

568

569 James, C. S., Capon, S. J., White, M. G., Rayburg, S. and Thomas, M. C. (2007) Spatial variability of the  
570 soil seed bank in a heterogeneous ephemeral wetland system in semi-arid Australia. *Plant Ecology*  
571 190(2): 205-217.

572

573 Kew RBG (2019) *MSB Seed List — Royal Botanic Gardens, Kew*. <http://apps.kew.org/seedlist>  
574 Accessed 5 May 2019.

575

576 Kingsford, R.T. (2000) Ecological impacts of dams, water diversions and river management on  
577 floodplain wetlands in Australia. *Austral Ecology* 25(2): 109-127.

578

579 Kemp, J. (2004) Flood channel morphology of a quiet river, the Lachlan downstream from Cowra,  
580 South-Eastern Australia. *Geomorphology* 60(1-2): 171-190.

581

582 Lenth, R. (2019) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package  
583 version 1.3.4. <https://CRAN.R-project.org/package=emmeans>

584

585 Leyer, I. (2006) Dispersal, diversity and distribution patterns in pioneer vegetation: the role of river-  
586 floodplain connectivity. *Journal of Vegetation Science* 17(4): 407-416.

587

588 Lu Z. J., Li L. F., Jiang M. X., Huang H. D. and Bao D. C. (2010) Can the soil seed bank contribute to  
589 revegetation of the drawdown zone in the Three Gorges Reservoir Region? *Plant Ecology* 209, 153-  
590 165.

591

592 Merritt D. M., Nilsson, C. and Jansson, R. (2010) Consequences of propagule dispersal and river  
593 fragmentation for riparian plant community diversity and interannual turnover. *Ecological*  
594 *Monographs* 80, 609-626.

595

596 Miller, K. A., Webb, A., de Little, S. C. and Stewardson, M. (2013) Environmental flows can reduce the  
597 encroachment of terrestrial vegetation into river channels: a systematic literature review.  
598 *Environmental Management* 52: 1201-1212.

599

600 Nielsen, D. L., Campbell, C., Rees, G. N., Durant, R., Littler, R. and Petrie, R. (2018) Seed bank  
601 dynamics in wetland complexes associated with a lowland river. *Aquatic Sciences* 80(2): 23.

602

603 Nilsson, C. and Svedmark, M. (2002) Basic principles and ecological consequences of changing water  
604 regimes: riparian plant communities. *Environmental Management* 30(4): 468-480.

605  
606 O'Donnell, J., Fryirs, K. and Leishman, M.R. (2013) Digging deep for diversity: riparian seed bank  
607 abundance and species richness in relation to burial depth. *Freshwater Biology* 59(1): 100-113.  
608  
609 O'Donnell, J., Fryirs, K. and Leishman, M.R. (2015) Can the regeneration of vegetation from riparian  
610 seed banks support biogeomorphic succession and the geomorphic recovery of degraded river  
611 channels? *River Research and Applications* 31(7): 834-846.  
612  
613 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R., Simpson, G.L, Solymos,  
614 P., Stevens, M.H.H. and Wagner, H. (2013) Package 'vegan'. Community ecology package, version  
615 2(9).  
616  
617 Poff, N., Allan, J., Bain, M., Karr, J., Prestegard, K., Richter, B., Sparks, R and Stromberg, J. (1997) The  
618 Natural Flow Regime. *BioScience*, 47(11): 769-784.  
619  
620 Poiani, K. A. and Johnson, W. C. (1988) Evaluation of the emergence method in estimating seed bank  
621 composition of prairie wetlands. *Aquatic Botany* 32(1-2): 91-97.  
622  
623 Richardson, F. J., Richardson, R. G. and Shepherd, R. C. H. (2016) *Weeds of the South-east: An*  
624 *Identification Guide for Australia* (Ed. 3). CSIRO.  
625  
626 Reid, M. and Capon, S. (2011) Role of the soil seed bank in vegetation responses to environmental  
627 flows on a drought-affected floodplain. *River System* 19(3): 249–259  
628  
629 Royal Botanic Gardens Victoria (2019). *Flora of Victoria*. <https://vicflora.rbg.vic.gov.au/flora/search>  
630 Accessed 1 Jun. 2019.  
631  
632 Siebentritt, M. A., Ganf, G. G. and Walker, K. F. (2004) Effects of an enhanced flood on riparian  
633 plants of the River Murray, South Australia. *River Research and Applications* 20(7): 765-774.  
634  
635 Soons, M. B., de Groot, G. A., Cuesta Ramirez, M. T., Fraaije, R. G., Verhoeven, J. T. and de Jager, M.  
636 (2017) Directed dispersal by an abiotic vector: wetland plants disperse their seeds selectively to  
637 suitable sites along the hydrological gradient via water. *Functional Ecology* 31(2): 499-508.  
638  
639 Stokes, K., Ward, K. and Colloff, M. (2010) Alterations in flood frequency increase exotic and native  
640 species richness of understorey vegetation in a temperate floodplain eucalypt forest. *Plant*  
641 *Ecology* 211(2): 219-233.  
642  
643 Thompson, K. and Grime, J. P. (1979) Seasonal variation in the seed banks of herbaceous species in  
644 ten contrasting habitats. *The Journal of Ecology*: 893-921.  
645  
646 Thompson, K., Band, S. R. and Hodgson, J. G. (1993) Seed size and shape predict persistence in  
647 soil. *Functional Ecology*: 236-241.  
648  
649 Tonkin, Z., Jones, C., Clunie, P., Vivian, L., Amtstaetter, F., Jones, M., Koster, W., Mole, B., O'Connor,  
650 J., Brooks, J., Caffrey, L., and Lyon, J. (2020). Victorian Environmental Flows Monitoring and  
651 Assessment Program. Stage 6 Synthesis Report 2016-2020. Technical Report Series No. 316,  
652 Department of Environment, Land, Water and Planning, Heidelberg, Victoria.  
653

- 654 Vietz, G. J., Rutherford, I. D. and Stewardson, M. J. (2004) Not all benches are created equal:  
655 Proposing and field testing an in-channel river bench classification. In *Proceedings of the 4th*  
656 *Australian Stream Management Conference*. Department of Primary Industries, Water and  
657 Environment, Launceston Tasmania.
- 658
- 659 Wei, Y., Langford, J., Willett, I. R., Barlow, S. and Lyle, C. (2011) Is irrigated agriculture in the Murray  
660 Darling Basin well prepared to deal with reductions in water availability? *Global Environmental*  
661 *Change* 21(3): 906-916
- 662
- 663 Williams, L., Reich, P., Capon, S. J. and Raulings, E. (2008) Soil seed banks of degraded riparian zones  
664 in southeastern Australia and their potential contribution to the restoration of understorey  
665 vegetation. *River Research and Applications* 24(7): 1002-1017.

666

## Supplementary material

667

668

**Table S1: List of study sites where seedbank samples were collected and their GPS coordinates**

Site Number	Site Name	GPS Coordinates
1	Doaks Reserve	-36.816101, 144.517646
2	English Bridge	-36.619369, 144.563227
3	Bryants Lane	-36.411715, 144.668521
4	Spencer Road	-36.380974, 144.708964
5	Strathallan Road	-36.256020, 144.735310
6	Campbell Road	-36.172852, 144.747545

669

670

**Table S2: List of identified taxa across all study sites and studied geomorphic features, including their flood tolerance, origin, growth form, total seedling abundance and site number that the species was recorded in the extant vegetation close to the sample sites.**

671

672

Species	Flood Tolerant	Origin	Growth Form	Seedling Abundance	Extant within site no.
<i>Acetosella vulgaris</i>	Yes	Exotic	Forb	1	-
<i>Alternanthera denticulata</i>	Yes	Native	Forb	2	1, 2, 3, 4, 5, 6
<i>Arctotheca calendula</i>	No	Exotic	Forb	8	1, 2, 5
<i>Aster subulatus</i>	Yes	Exotic	Forb	11	1, 2, 3
<i>Brachypodium distachyon</i>	No	Exotic	Grass	18	1, 2, 3, 4, 6
<i>Bromus catharticus</i>	No	Exotic	Grass	95	1, 2, 4, 6
<i>Callistemon sieberi</i>	Yes	Native	Shrub	1	1, 3, 4
<i>Cardamine hirsuta</i>	Yes	Exotic	Forb	4	-
<i>Carex</i> spp.*	Yes	Native	Sedge	400	1, 2, 3, 4, 5, 6
<i>Centaurium erythraea</i>	No	Exotic	Forb	10	1, 2
<i>Centipeda cuttinghamii</i>	Yes	Native	Forb	7	-
<i>Cerastium glomeratum</i>	No	Exotic	Forb	1	-
<i>Cirsium vulgare</i>	No	Exotic	Forb	2	1, 2, 3, 4, 5, 6
<i>Crassula helmsii</i>	Yes	Native	Forb	75	1, 2
<i>Crassula decumbens</i>	No	Native	Forb	2	-
<i>Cullen parvum</i>	No	Native	Forb	4	4, 5
<i>Cyperus eragrostis</i>	Yes	Exotic	Sedge	661	1, 2, 3, 4, 5, 6
<i>Dactylis glomerata</i>	No	Exotic	Grass	2	1, 2
<i>Dysphania pumilio</i>	No	Native	Forb	26	1, 5, 6
<i>Epilobium billardierianum</i>	No	Native	Forb	2	1
<i>Erharta longiflora</i>	No	Exotic	Grass	13	1, 2, 4, 6
<i>Eucalyptus camaldulensis</i>	Yes	Native	Tree	10	1, 2, 3, 4, 5, 6
<i>Euchiton japonicus</i>	No	Native	Forb	94	1, 2
<i>Euphorbia dallachyana</i>	No	Native	Forb	1	3, 5, 6
<i>Helichrysum luteoalbum</i>	No	Native	Forb	57	1, 5
<i>Heliotropium europaeum</i>	No	Exotic	Forb	12	2, 6
<i>Isolepis levynsiana</i>	Yes	Exotic	Sedge	21	1
<i>Juncus</i> spp.**	Yes	Native	Rush	3778	1, 2, 3, 4, 5, 6
<i>Juncus prismatocarpus</i> ***	Yes	Native	Rush	62	1, 2

Species	Flood Tolerant	Origin	Growth Form	Seedling Abundance	Extant within site no.
<i>Lachnagrostis filiformis</i>	Yes	Native	Grass	588	1, 2, 3, 4, 5, 6
<i>Lepidium</i> sp.	No	Exotic	Forb	1	1
<i>Lolium</i> spp.	No	Exotic	Grass	93	1, 2, 3, 4, 5, 6
<i>Lythrum hyssopifolia</i>	Yes	Native	Forb	5	1, 2, 3
<i>Myriophyllum</i> sp.	Yes	Native	Forb	1	1, 2
<i>Oxalis perennans</i>	No	Native	Forb	24	1, 2, 3, 4, 5, 6
<i>Oxalis pes-caprae</i>	No	Exotic	Forb	7	1, 2, 3, 4, 5, 6
<i>Panicum coloratum</i>	Yes	Exotic	Grass	17	3, 4, 5, 6
<i>Paspalum distichum</i>	Yes	Native	Grass	30	1, 2, 3, 4, 5
<i>Persicaria hydropiper</i>	Yes	Native	Forb	33	1, 2
<i>Persicaria prostrata</i>	Yes	Native	Forb	26	1, 2, 3, 4, 5, 6
<i>Petrorhagia nanteuilii</i>	No	Exotic	Forb	2	-
<i>Plantago lanceolata</i>	No	Exotic	Forb	79	3, 4, 5
<i>Plantago major</i>	No	Exotic	Forb	1	-
<i>Polygonum aviculare</i>	No	Exotic	Forb	2	1, 2, 5
<i>Poranthera microphylla</i>	No	Native	Forb	2	-
<i>Ranunculus sceleratus</i>	Yes	Exotic	Forb	1	-
<i>Romulea rosea</i>	No	Exotic	Forb	36	1, 2, 3, 4, 5, 6
<i>Rumex brownii</i>	Yes	Native	Forb	1	1, 2, 3, 4, 5, 6
<i>Rytidosperma</i> spp.	No	Native	Grass	22	1, 2, 3, 4, 5, 6
<i>Sonchus oleraceus</i>	No	Exotic	Forb	4	1, 2, 3, 4
<i>Trifolium angustifolium</i>	No	Exotic	Forb	1	6
<i>Trifolium repens</i>	No	Exotic	Forb	30	1
<i>Typha domingensis</i>	Yes	Native	Grass	35	2
<i>Verbena officinalis</i>	No	Native	Forb	6	4, 5
<i>Vulpia bromoides</i>	No	Exotic	Grass	90	1, 2, 3

673

674 \* Taxa consisting of two phenologically similar native perennial sedges: *Carex appressa* and *C.*  
675 *gaudichaudiana*

676 \*\* Taxa consisting of two phenologically similar native perennial rushes: *Juncus amabilis* and *J.*  
677 *usitatus*.

678 \*\*\* There is a reasonable chance that *Juncus articulatus* was also present within the soil seedbank  
679 samples collected but was misidentified as *Juncus prismatocarpus* in some cases.

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