

Flood disturbance affects morphology and reproduction of woody riparian plants

Sarah Fischer (✉ fischers@student.unimelb.edu.au)

University of Melbourne

Joe Greet

University of Melbourne

Christopher Walsh

University of Melbourne

Jane Catford

King's College London

Research Article

Keywords: tree structure, wetland forest, resprouting-reseeding, multi-stemmed, flood regime

Posted Date: April 15th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-403578/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at Scientific Reports on August 13th, 2021.

See the published version at <https://doi.org/10.1038/s41598-021-95543-0>.

FLOOD DISTURBANCE AFFECTS MORPHOLOGY AND REPRODUCTION OF WOODY RIPARIAN PLANTS

Authors¹: Sarah Fischer¹, Joe Greet¹, Christopher J. Walsh¹, Jane A. Catford^{2,3}

Institutional affiliations: ¹School of Ecosystem and Forest Sciences, Burnley Campus, The University of Melbourne, Burnley, Victoria, Australia; ²Department of Geography, King's College London, London, WC2B 4BG, UK; ³School of BioSciences, University of Melbourne, Victoria, 3010, Australia.

Contact details for corresponding author: Sarah Fischer, rettichretter@hotmail.de, 0061448049172

¹ Declaration of authorship

SF, JG, CW and JC conceived the study and developed the methodology. SF and JG conducted the fieldwork. SF, JG and CW analysed the data. SF wrote the main manuscript text; all other authors reviewed the manuscript and provided editorial advice.

1 **Abstract**

2 Riparian forests are structured and maintained by their hydrology. Woody riparian plants typically adapt
3 to the local flood regime to maximise their likelihood of survival and reproductive success. Understanding
4 how extant trees form and reproduce in response to flood disturbance is crucial for predicting vegetation
5 changes and informing restoration. Working in a temperate evergreen riparian forest, we aim to
6 determine whether disturbance-based responses of plants found in other ecosystems also typify woody
7 plants in riparian forests where disturbances are non-lethal, annual events.

8 Using plant surveys and 20-year modelled hydrological data, we examined whether i) the morphology
9 (main stem diameter, height, crown width, crown extent, stem leaning) and ii) reproduction type (sexual
10 and asexual reproduction) and extent of three dominant woody species (*Eucalyptus camphora*,
11 *Leptospermum lanigerum* and *Melaleuca squarrosa*) vary with flood regime (flood frequency and flood
12 duration); and iii) whether different morphology is associated with different reproductive strategies.

13 Increased flooding generally resulted in increased stem numbers and greater stem leaning – morphologies
14 associated with asexual reproduction – of our study species. More frequent flooding also reduced plant
15 size and sexual reproduction in *E. camphora*. Sexual reproduction in the studied species was more
16 common in taller plants with single, more upright stems in good condition.

17 Flexible morphology and plastic reproductive strategy may constitute an adaptation to mild or chronic
18 disturbance in floodplains. Our findings suggest that woody plants respond to physical disturbance in
19 consistent ways regardless of the nature of the disturbance – be it fires, hurricanes or floods.

20

21 **Keywords:** tree structure, wetland forest, resprouting-reseeding, multi-stemmed, flood regime

22 **Introduction**

23 Healthy riparian forests control sediment runoff, purify water, stabilize banks, regulate stream
24 temperatures and are home to considerable biodiversity. As they are large and abundant, the physical
25 form of trees and shrubs is pivotal to the overall structure and function of forests. A remarkable feature
26 of woody plants is their flexible morphology in response to their environment [1]. In forested floodplains,
27 hydrology poses a major shaping force on tree and shrub development. Once established, woody plants
28 adjust energy and resource allocations to survival, growth and reproduction in response to the flood
29 regime, increasing their longevity and likelihood of reproductive success[1, 2]. With increasing human
30 impacts globally, anthropogenic flow regulation has disrupted the natural water fluctuations under which
31 riparian forests have evolved, leading to their decline [3]. The resulting negative consequences for the
32 environment and society have motivated efforts to actively restore riparian ecosystems. However,
33 inducing such recovery requires sound understanding of woody plant responses to flood regime.

34 Challenges in ascertaining hydro-biological relationships arise from the diverse responses of plants to
35 flooding [4]. On the one hand, regular flooding can provide plentiful water and nutrients, which usually
36 supports tree growth [5]. On the other hand, periods of flooding may cause physical stress resulting from
37 flowing water and smothering by sediments, which potentially causes stem breakage or forces plants into
38 leaning positions. Moreover, physiological stress may arise from waterlogging and soil anoxia and toxicity
39 [6, 7]. Although riparian plants can often withstand such unfavourable conditions, metabolic costs for
40 survival and recovery typically enforces limited growth and size [8]. Branch dieback and regrowth shapes
41 the crown architecture and overall growth shape of trees [9]. Responses may differ among co-occurring
42 woody plants depending on species-specific adaptations, growth form and phenological cycles [10, 11].

43 Previous research on vegetation responses to flooding have typically focused on survival, adaptive traits,
44 growth (e.g. of stem diameter or biomass) or vegetation community composition [12-15]. Tree

45 morphology has received little attention outside forestry, despite its significance for ecosystem structure
46 and function [16], and there is a particular lack of empirical evidence from evergreen temperate riparian
47 species. Trees embody their individual life history in their form. Understanding how extant trees have
48 formed and regenerate in response to past flood regimes may provide valuable information for restoring
49 adequate conditions (i.e. flood regimes) to promote regeneration and the development of desired forest
50 structures.

51 Morphologic plasticity of perennial species in response to environmental factors has been well
52 documented in other disturbance-prone ecosystems: mainly in those disturbed by fire [17], but also in
53 areas affected by catastrophic winds, landslides, avalanches [18-20] and ephemeral and saline wetland
54 systems [4, 9, 21]. Different morphologies are often associated with different reproductive strategies
55 which are in turn influenced by the nature of the disturbance regime [22]. Two alternative strategies used
56 by plants have been identified to maintain populations in disturbance-prone environments, namely
57 resprouting and reseedling [23], often also referred to as vegetative or asexual, and sexual reproduction
58 [24]. Multi-stemmed, mostly smaller individuals often occur at sites with more disturbance and originate
59 from and pursue vegetative persistence, whereas sexual or seed-based reproduction is more frequent in
60 taller, usually single-stemmed individuals which experience less disturbance (Fig. 1). To date, the
61 relationship between disturbance, morphology and reproductive strategy for woody plants in riparian
62 forests remains unclear.

63 In this study, we aim to determine whether the disturbance-based responses of plants found in other
64 ecosystems also typify woody plants in riparian forests where disturbances are moderate (i.e. do not
65 destroy or damage the majority of a plant's biomass in one event) and occur regularly (e.g. seasonally
66 each year). We surveyed morphological characteristics and extent of sexual and asexual reproduction in
67 three woody riparian species in an evergreen temperate forest and examined their association with
68 modelled, long-term flooding data to test the following hypothesis (Fig. 1):

69 (H1) Morphology (main stem diameter, height, crown width, crown extent, stem leaning) varies with flood
70 regime (flood frequency and flood duration);

71 (H2) Reproduction type (sexual and asexual reproduction) and extent are plastic in response to flood
72 regime;

73 (H3) Different morphology is associated with different reproductive strategies.

74

75 **Methods**

76 *Study site*

77 Our study was undertaken in the Yellingbo Nature Conservation Reserve located around 45 km east of
78 Melbourne, Victoria, Australia. The reserve is embedded in an agricultural landscape and is around 640
79 ha comprising narrow riparian zones bordering local creeks. Low-lying floodplains along the Cockatoo and
80 Macclesfield Creeks, which were focus of our surveys, are dominated by ‘Sedge-rich *Eucalyptus camphora*
81 Swamp’ community [25]. These forests naturally experience seasonal to near-permanent inundation and
82 vary in structure from open forest to woodland. The highly flood-tolerant mountain swamp gum
83 *Eucalyptus camphora* is the sole overstorey species. The midstorey is dominated by thickets of woolly tea
84 tree *Leptospermum lanigerum* and scented paperbark *Melaleuca squarrosa*, both of which are flood
85 tolerant small trees or shrubs [26]. The largest remnants of this forest type are found within the Yellingbo
86 Nature Conservation Reserve where they suffer dieback as a result of past human alterations of local
87 watercourses [27]. The long-term survival of this threatened riparian forest likely depends on
88 management interventions. Despite thorough documentation of declining tree and shrub condition, the
89 ecology of the three major woody species is not well understood [28, 29].

90

91 *Survey design*

92 We confined the survey area to elevations lower than 120 m above sea level as *Eucalyptus camphora*
93 swamp does not occur above this elevation within the reserve [26]. Only areas mapped as vegetation
94 communities containing the studied species were included. The survey area was further limited to match
95 the extent of a hydrological model (see below) and was in total 1.69 km².

96 In order to ensure that survey points were distributed across the hydrological gradient, we simulated
97 different sized flooding events using a hydrologic model (described below). The spatial extents of these

98 events were then used to classify the study area into four broad flooding categories. Flooding categories
99 one, two and three comprised areas which were flooded by low, medium and high flow events,
100 respectively. Flooding category one represents the wettest parts of the floodplain whereas categories two
101 and three are less frequently flooded. Flooding category four contained the rarely inundated parts of the
102 survey area that remained unflooded in the modelled flow events.

103 To equally represent all flooding categories, we used a stratified random sampling approach. We
104 generated 40 random coordinates within the area represented by each category and four additional
105 points per point were generated as spares in case some positions were unsuitable for sampling.

106 During field surveys, we visited locations by navigating with a handheld GPS device (Garmin etrx30) to the
107 predefined points. From there, we surveyed the nearest individual of each of the species *E. camphora*, *M.*
108 *squarrosa* and *L. lanigerum* and mapped their actual geographic position. If no tree was found within a
109 radius of 10 m of a given sample point, we visited the closest point from the spare dataset instead. If no
110 individual was present near any of the four closest spare points no tree was recorded at the location.

111 After visiting all of the original points (including the four extra points) additional points were generated
112 randomly in the areas where the two shrub species were found during the course of previous sampling.
113 We thereby increased sample size for each of these less widespread species to at least 20 individuals per
114 flooding category. We conducted all surveying and tree and shrub measurements from March to April
115 2018 to take advantage of low water levels and therefore best accessibility. In total, we sampled 292 trees
116 comprising 133 *E. camphora*, 78 *L. lanigerum* and 84 *M. squarrosa*.

117

118 *Tree surveys*

119 Elongated stems are a major feature of woody plants defining their overall architecture. To characterise
120 and compare growth habits, we measured diameter at breast height (DBH) and height (to highest live
121 foliage) of each tree and shrub. In some cases (for 21/133 *E. camphora* and 1/84 *L. lanigerum*) visibility
122 impairment precluded height measurement via clinometer. For multi-stemmed individuals, we counted
123 all stems, measured their DBH, and determined height of the tallest one. To yield crown width we
124 measured maximum crown diameter and perpendicular crown diameter for every sampled plant and
125 calculated the mean.

126 Flooding and associated unstable, boggy substrates might deter trees from the usual vertical growth and
127 force them into leaning positions. Thus, we recorded inclination angle of the main stem relative to vertical.

128 The emergence of epicormic sprouts, be it a symptom of stress or sign of recovery [30], is a common
129 reaction to disturbance and reflects a tree's ability to regenerate vegetatively. We estimated epicormic
130 growth using a scale from 0–3 indicating absent, scarce, common or abundant expression of epicormic
131 growth [31].

132 Using the same scale, we assessed sexual reproduction by estimating the combined relative abundance
133 of reproductive structures, namely buds, flowers and capsules. Flowers indicate only current reproductive
134 activity and not all species were flowering during the fieldwork campaign. Owing to serotiny and the long
135 timespan for bud crop development, different developmental stages of reproductive structures (current
136 and past reproduction) can appear simultaneously on a single tree.

137 Growth and reproduction may both be affected by plant condition, for which crown vigour has been
138 proven as a suitable and rapid measure [21, 30]. For each sampled plant, we assessed crown vigour by
139 visually estimating the proportion of the potential crown supporting live foliage to the nearest 5%.

140 Moreover, growth rates and tree shapes can be significantly influenced by competition. For each sampled
141 tree or shrub, we therefore measured the distances to its nearest four neighbours, one in each compass

142 quadrant and calculated the average nearest-neighbour distance. For *E. camphora*, only neighbouring
143 trees were included, whereas for *L. leptospermum* and *M. squarrosa* trees and shrubs were considered
144 neighbours.

145 *Hydrologic Modelling*

146 After completing tree surveys, we determined local flood regime history for each study tree using the
147 output of a grid-based, 2-dimensional hydrological model built in TUFLOW classic (www.tuflow.com),
148 which was calibrated with recent water-level data from four sites within the study area. The model
149 generated historic-flow series (1998–present) of water levels across the study area with a 5-m grid-cell
150 spatial resolution and a daily temporal resolution. See Greet, Fischer [32] for more details.

151 We extracted water-level time series for each surveyed tree and shrub from the model output. Using the
152 recorded coordinates, individual water-level data were extracted for the grid cell in which the respective
153 tree or shrub was located. Some individuals that were located next to the stream were allocated to a grid-
154 cell that the model designated as the stream channel, resulting in them being erroneously characterised
155 as permanently inundated. In these cases, water level data was extracted for the eight surrounding cells.
156 We then excluded those that were also permanently inundated, and the average of the remaining cells
157 was used to create a water level time series for that individual.

158 To characterise the flood regime history for each tree, we considered water levels of zero as dry and values
159 greater than zero as inundated. Therefore, the first day with a water level greater zero marked the start
160 of a flooding event and the reduction to zero the end of the respective event. Consequently, the number
161 of consecutive days of flooding defined the length of a flooding event.

162 We calculated the following flood regime metrics for the modelled 20-year period (1998-2018): mean and
163 maximum length of flooding periods, mean and maximum length of dry spells (not inundated periods),
164 the mean length of flooding periods during the growing season (November to June), the average number

165 of flooding events per year and mean flooding depth. All variables were skewed and thus log-transformed
166 before we tested for correlation (Online Resource 1, Fig. SM1). We assumed the observed flooding
167 magnitude, i.e. mean water levels (mean= 0.06 cm, median= 0.01 cm, max=0.92 cm), to be less important
168 for the relatively tall trees and shrubs studied here. We further assumed maximum values to be less
169 influential for tree and shrub growth over long periods. Hence, we selected two contrasting aspects
170 characterizing long-term flood regime as predictors for further statistical analysis. These were the mean
171 length of flooding events and the average number of flooding events per year representing duration and
172 frequency of flooding. They were not strongly correlated with each other (Pearson correlation coefficient
173 = 0.18).

174 14 out of 292 sampled trees from across the study area were excluded from statistical analyses due to
175 model outputs suggesting unrealistic high flood duration (i.e. mean inundation duration > 500 days) or
176 frequency (i.e. > 300 events), likely owing to errors of local topography representation based on our field
177 observations.

178 *Statistical analysis*

179 We performed multiple regression separately for each of the three species to:

180 i) assess the strength of relationships between flood regime (flood frequency, flood duration) and tree
181 and shrub morphology (DBH of main stem, height, crown width, stem number, leaning and crown extent);
182 and flood regime and reproductive strategy (the extent of sexual reproduction and epicormic growth),
183 thereby testing hypothesis 1 and 2 (H1 and H2); and

184 ii) and the relationships between morphology and both reproduction types, testing hypothesis 3 (H3).

185 For each analysis we used hierarchical partitioning to identify those variables which independently
186 explained the most variance in morphology and reproduction, respectively.

187 First, we tested how much variation in morphology and reproductive strategy variables was explained by
188 each of the two flood regime variables (H1 and H2). We fit 8 generalised linear models (response variables:
189 main stream DBH, height and crown width, stem number, leaning, crown extent, sexual reproduction, and
190 epicormic growth; predictor variables: flood frequency, flood duration). We chose the appropriate
191 distribution used in the linear model for each variable (Table 1). Beta regression was undertaken using
192 the *betareg* package [33] and ordinal regression using the *MASS* package [34].

193 We initially included the average nearest neighbour distance (a surrogate for competition) in models
194 predicting morphology variables (H1). However, we later omitted this additional predictor as it generally
195 did not increase the proportion of explained variance (Online Resource 2, Table SM1).

196 To assess how much variation in reproductive strategy variables was explained by morphology variables
197 (H3), for each species, we calculated two additional linear models for the response variables of sexual
198 reproduction and epicormic growth with each six predictor variables (main stem DBH, height, crown
199 width, stem number, leaning and crown extent). Both of these models used a binomial distribution
200 adapted for ordered factors.

201 For each model, we used hierarchical partitioning of log-likelihood values using the *hier.part* package [35]
202 to determine the proportion of explained variance explained independently by each predictor variable
203 [36]. This method allows identification of variables that have a strong independent correlation with the
204 dependent variable, in contrast to variables that have little independent effect but have a high correlation
205 with the dependent variable resulting from joint correlation with other predictor variables. Variables that
206 independently explained a larger proportion of variance than could be explained by chance were
207 identified by comparison of the observed value of independent contribution to explained variance (I) to a
208 population of I s from 1000 randomizations of the data matrix. Significance was accepted at the upper 95%
209 confidence limit (Z -score > 1.65 : Mac Nally 2002[37], Mac Nally and Walsh 2004).

210 To assess the goodness of fit for each model, we present R^2 or pseudo- R^2 values (according to Nagelkerke
211 using the DescTools package: Signorell *et al.*, 2019[38]) for ordinal regression and Ferrari and Cribari-Neto
212 (2004) for beta regression, respectively. We considered variables with a total contribution to explained
213 variance (i.e. proportion explained $\times R^2$) > 0.05 to be influential variables and the direction of their effect
214 important.

215 Lastly, we performed a PCA analyses and ordination to assess associations between different morphology
216 attributes and reproduction variables across all species (H3).

217 All statistical analysis was performed in R version 3.5.0. [39].

218

219 Results

220 All species were similarly distributed across the hydrological gradient based on flood duration and
221 frequency (Online Resource 3, Fig. SM2, Online Resource 4, Table SM2). However, *E. camphora* was more
222 spatially widespread, whereas both shrub species had patchier distributions within the study area (Fig. 2).
223 Three morphology attributes (main stem DBH, tree height, and crown width) were more variable for the
224 taller species *E. camphora* than for *L. lanigerum* and *M. squarrosa* (Fig. 3a, b and c, Online Resource 4,
225 Table SM2). Condition varied widely in all species (Fig. 3d). Multi-stemmed growth was more common in
226 the shrub species than *E. camphora* (Fig. 3e). Stem leaning was generally frequent albeit to varying
227 degrees (Fig. 3f). More than 90% of trees and shrubs showed some evidence of sexual reproduction
228 (Online Resource 5, Fig. SM3a). Such evidence was common or abundant in 60% of *E. camphora* trees
229 surveyed, but in both shrub species, evidence of sexual reproduction was mostly scarce (51% in *L.*
230 *lanigerum*, 73% in *M. squarrosa*, Online Resource 5, Fig. SM3a). Epicormic growth was prevalent in all
231 species with more than 50% of individuals of all three species displaying common or abundant epicormic
232 growth (Online Resource 5, Fig. SM3b). *M. squarrosa* exhibited the highest extent of epicormic growth
233 (68% common or abundant).

234

235 *H1 and H2: Association between flood regime and plant morphology and reproduction*

236 Flood regime explained a modest amount of variation in morphology and reproductive strategy variables
237 (maximum R^2 of 0.27 for *M. squarrosa* stem number, Table 2), providing partial support for H1 and H2.
238 More associations between flood regime and morphology and reproduction were found for *E. camphora*
239 (six variables) than for *L. leptospermum* and *M. squarrosa* (two and three variables, respectively).
240 Flood frequency was a consistently strong contributor to explained variance in growth-form variables and
241 reproduction in *E. camphora* (Table 2). Trees experiencing more frequent flooding tended to have thinner

242 main stems (Fig. 4a), be shorter (Fig. 4b) and have greater numbers of stems (Fig. 4c), and they tended to
243 lean more (Fig. 4d), less commonly show evidence of sexual reproduction (Fig. 4f) and display more
244 epicormic growth (Fig. 4g). Leaning was the only variable for which flood duration had a strong
245 independent contribution to explained variance. Stem leaning was more pronounced in *E. camphora* in
246 locations with longer periods of flooding (Table 2, Fig. 4e).

247 For the shrub species, flood duration was more commonly a strong contributor to explained variance.
248 Both *L. lanigerum* and *M. squarrosa* subjected to longer flooding tended to have more stems (Fig. 4h, k),
249 and *M. squarrosa* tended to lean more and have more epicormic growth in locations with longer floods
250 (Fig. 4l, m). In addition, flood frequency was a strong contributor to explained variance for leaning of *L.*
251 *lanigerum* (more leaning with more frequent floods, Fig. 4i), and for stem number of *M. squarrosa* (more
252 stems with more frequent floods, Fig. 4j).

253 We did not find evidence for an effect of flood duration or frequency on the condition (crown extent) or
254 crown width of any species (Table 2).

255

256 *H3: Associations between morphology and reproduction type and extent*

257 For all species, a larger proportion of variation in reproduction was explained by morphology than by flood
258 regime (Table 2, Table 3). In general, main stem DBH, stem leaning, and crown extent had high
259 contributions to the explained variance in sexual reproduction and epicormic growth, providing support
260 for H3 (Table 3).

261 Individuals with higher main stem DBH showed higher extents of sexual reproduction in *E. camphora* and
262 *L. leptospermum* (Fig. 5a, c, Table 3), whilst *M. squarrosa* with larger stem diameters had more epicormic
263 growth (Fig. 5g, Table 3).

264 Higher degrees of stem leaning were associated with less sexual reproduction in *L. leptospermum* (Fig. 5e,
265 Table 3) and more epicormic growth in *E. camphora* (Fig. 5b, Table 3).

266 *M. squarrosa* in better condition had higher extents of sexual reproduction (Fig. 5f, Table 3), whereas *L.*
267 *leptospermums* in lower condition had more epicormic growth (Fig. 5d, Table 3).

268 The first two axes of the PCA explained 56.1% of the variation in morphology and reproduction attributes
269 of all three species and show the attributes of the larger tree species, *E. camphora*, to be somewhat
270 distinct from the other two species (Online Resource 6, Fig. SM4). Across the three species, the two
271 reproductive strategies are negatively correlated and associated with divergent morphology which
272 provides further support for H3. Multi-stemmed form and stem leaning is associated with asexual
273 reproduction (epicormic growth), while sexual reproduction is associated with greater plant size (main
274 stem DBH and height).

275 Discussion

276 By examining relationships between flood regime, morphology and reproductive strategy of three
277 dominant riparian woody plants, we found support for all of our three hypothesis: flood frequency and
278 duration influenced woody riparian plant morphology (H1) and reproduction (H2), and different
279 morphology was associated with different reproductive strategies (H3). Increased flooding generally
280 resulted in increased stem numbers and greater stem leaning of our study species; this morphology was
281 associated with asexual reproduction. More frequent flooding also reduced size and sexual reproduction
282 in *E. camphora*. Sexual reproduction was more common in taller plants with single, more upright stems in
283 good condition. Our findings suggest that woody plants respond to physical disturbance in a similar set of
284 ways regardless of the nature of that disturbance – be it fires, hurricanes, avalanches or moderate, regular
285 disturbance by floods. Interestingly, the morphology and reproduction of our three study species were
286 affected by different aspects of the flood regime (flood frequency cf. duration). This indicates that flood
287 regime (i.e. variable frequency and duration of flooding events) is critical to the structural integrity and
288 self-maintenance of species-diverse riparian forests.

289

290 *H1: Morphology is plastic in response to flooding*

291 Apart from being a stress response and survival mechanism, the morphological plasticity we found in our
292 study species may constitute an adaptation to mild or chronic disturbance. Evergreen species that do not
293 have marked seasonal growth interruptions may lack the ability to avoid flood stress via dormancy and
294 thus require a high level of adaptation to cope with physical and physiological stress [40]. Adaptive traits
295 conferring flood tolerance and the physiological mechanisms underpinning morphological changes are
296 manifold [7], and co-occurring species may respond to different attributes of the flood regime [41]. In our
297 study the more flood tolerant species, *L. lanigerum* and *M. squarrosa* [29], seemed less sensitive to

298 frequent flooding and their morphology responses tended to occur with longer duration floods.
299 Conversely, *E. camphora* initiates more immediate responses to flooding [28] and its morphological
300 variability was more strongly associated with flood frequency. As documented elsewhere, we found the
301 morphology of shrubs to be less impacted by disturbance than trees [20], but also to be less variable than
302 trees overall. Growth rates of the shrub species studied here (*L. lanigerum* and *M. squarrosa*) were
303 previously shown to respond in a non-linear manner to increased water levels [29] and this may also apply
304 to their morphology responses.

305 Consistent with patterns found in other wetlands, we found an increased prevalence of multi-stemmed
306 growth with increased flooding [4, 42, 43]. Although many plants possess the ability to resprout,
307 resprouting typically requires environmental disturbance [23]. This often follows, but does not necessarily
308 require, visible plant damage [44]. Suppressed root and shoot growth during flooding or mechanical stress
309 may alter internal hormone balance [13, 44]. Consequently, reduced apical dominance, the hormonally
310 regulated prevailing growth of the main stem, facilitates emergence of epicormic sprouts [45] and
311 therefore stem multiplication. A larger number of stems increases an individual's surface area usable for
312 stem gas exchange and therefore potentially enhances oxygen transport to roots during soil anoxia under
313 inundation [4]. Besides, possessing a plurality of usually smaller stems reduces the mortality risk due to
314 stem damage, in part because smaller stems are less prone to mechanical perturbation [46].

315 Repeated physical perturbation from flowing water and prolonged waterlogging likely cause stem leaning
316 of woody plants, such as we observed. As shown in other disturbance prone ecosystems, the upright
317 growth of woody stems can be compromised by external mechanical stresses such as avalanches or
318 substrate movements [19, 20]. In addition, longer flood durations induce soil softening and thus can
319 diminish anchorage and, while preventing excessive root breakage, cause plant tilting. This might
320 especially be the case in combination with strong winds. Thereby larger species, such as *E. camphora* (but

321 also *M. squarrosa*), provide more surface area and are likely exposed to higher wind speeds and are
322 therefore more vulnerable to being blown over.

323 Slow growth, compromised stability and altered morphology due to flooding might limit the size of *E.*
324 *camphora*, the tallest of our study species. A typical characteristic of the tree growth habit is the pursuit
325 of reaching large size [1]. However, tree growth is typically hampered by prolonged flooding [32], as has
326 been previously observed in *E. camphora* when subjected to inundation in the field [47] and in greenhouse
327 experiments [28]. Accordingly, we found that the size of *E. camphora* was inversely related to flood
328 frequency, with smaller plants growing in areas with higher flood frequencies. Particularly under
329 reoccurring flooding disturbance, increase in size requires a larger proportion of photosynthetic
330 assimilates to be invested in structural support tissue [48, 49], which in turn slows growth [46]. Whereas
331 shrubs grow multi-stemmed even in the absence of disturbance, the distribution of biomass across
332 multiple stems in frequently flooded trees requires resource allocation changes at the cost of height
333 growth [50].

334 *H2 flooding induces reproductive strategy responses*

335 The extent of sexual reproduction decreased in *E. camphora* with increased flood frequency. Perhaps
336 because high maintenance costs, especially of larger species during or post disturbance, have diverted
337 resources away from the development of reproductive structures [51]. Diminished sexual reproduction
338 might have indirectly resulted from retarded growth due to flooding. The period of growing tall is a phase
339 of low reproduction in trees [49]. The reproductive phase is usually only entered after reaching a certain
340 size [1]. *E. camphora* at regularly flooded sites probably mature slowly. Shrub species in contrast mature
341 at smaller heights [11]. The size of *L. leptospermum* and *M. squarrosa* was not impacted by flooding and
342 likewise, neither was their sexual reproduction; yet, sexual reproduction in these shrubs was generally
343 low.

344 We found evidence that flooding encourages epicormic growth in *E. camphora* and *M. squarrosa*, which
345 might compensate for absent or limited sexual reproduction. Such vegetative reproduction, potentially
346 leading to multi-stemmed growth forms, is likely an essential survival mechanism, enabling rejuvenation,
347 longevity and persistence where recruitment success is low [23].

348 Our survey of both reproduction types reflected recently developed structures and this may explain the
349 relatively weak correlations with long-term flooding patterns we found. Unlike in fire prone ecosystems,
350 disturbances in riparian forests are typically milder, plant damage less severe and post disturbance
351 conditions less homogenous. Consequently reproduction responses in riparian trees and shrubs may be
352 more diverse and less obvious [8].

353 *H3 Reproductive strategy is associated with morphology*

354 Additional to environmental drivers, reproduction is regulated by intrinsic biological factors and hence we
355 found plants with contrasting morphology displayed contrasting reproductive strategies. Asexual and
356 sexual reproduction are thought to be traded-off against each other as resources required for resprouting
357 or resources stored to maintain resprouting ability are diverted from the production of reproductive
358 structures and vice versa [8, 52]. Consistent with observations from many woody species, we found sexual
359 reproduction increased with stem size in *E. camphora* and *L. leptospermum* [53, 54]. Investment in
360 reproduction might increase only after decelerating size increase [1] and larger individuals are more able
361 to expose seeds to dispersal vectors [55]. Plants struggling with stress may avert resources from flower,
362 fruit and seed production [21]. Accordingly, we found diminished sexual reproduction in leaning *L.*
363 *leptospermum* and in *M. squarrosa* in poorer conditions indicated by their crown extent.

364 Stem leaning is likely ecologically significant for the persistence and reproduction of *E. camphora* with its
365 treefall often resulting in new individuals [47]. The diversion from vertical to diagonal or horizontal
366 orientation can initiate trunk suckering and trigger the emergence of epicormic shoots [19]. Epicormic

367 growth serves to reconstruct lost biomass and optimize leaf positioning and light harvest post disturbance.
368 It can also be triggered by hormonal changes following partial dieback [21] and accordingly we found more
369 epicormic growth in *L. leptospermum* with declining condition. A requirement for epicormic growth is the
370 prevalence of stored resources as well as buds to resprout from [52]. For both, bigger stems can provide
371 a larger repository which might be the reason *M. squarrosa* with bigger stems displayed more epicormic
372 growth.

373 Unsurprisingly, and similar to many ecological field studies [9, 56], a large proportion of the variation in
374 morphology and reproduction remained unexplained by the assessed flood regime variables and
375 morphological attributes. Plant life processes, including morphology adaptations and reproduction,
376 respond to and are determined by a multiplicity of interacting biotic and abiotic factors, which likely
377 contributed noise to our data. Albeit simplifying complex water flows and fluxes, the modelled long-term
378 hydrological data at the individual tree level enabled high accuracy in characterizing flood regime which
379 is novel within ecological surveys [32]. This allowed us to uncover the diversity of functional responses of
380 co-occurring species to flooding, despite the complexity of the riparian environment.

381

382

383

384 *Conclusion*

385 Understanding the way in which hydrology impacts tree morphology and reproduction is crucial to predict
386 vegetation changes in a world with ever-increasing waterway modification. Among the multiple drivers of
387 degradation of riparian ecosystems, hydrology is one with the potential to be remediated by hydro-
388 geomorphic restoration (e.g. dam modification or controlled flooding). The structural complexity and

389 integrity of temperate riparian forests does not solely emerge from the presence or absence of its main
390 species but also requires appropriate flood regimes. Morphology supported by flooding, e.g. multi-
391 stemming and stem leaning, create dense stands and therefore specific microclimates and habitats for
392 swamp adapted flora and fauna [47, 57]. Our findings suggest that natural flooding regimes (i.e. frequent
393 and longer duration floods) are also pivotal for the initiation and long-term success of vegetative
394 reproduction, an important component of the self-maintenance of riparian woody species.

395

396 **Acknowledgments**

397 We acknowledge the Wurundjeri people as the Traditional Owners of the land on which the research was
398 undertaken. We thank Tony Lovell, Elise King, Vicky Waymouth, Christoph Hartmann, Alfie Lem, Roger
399 Sharp, Ezekiel James Kartinyeri and Luke Westerland for assistance with fieldwork.

400

401 **Declarations**

402 **Funding:** This research was funded by the Australian Research Council and partners Melbourne Water,
403 Parks Victoria, Zoos Victoria and Greening Australia (LP150100682). Funding was also provided by a
404 Holsworth Wildlife Research Endowment and an Australian Postgraduate Award to S. Fischer. Fieldwork
405 was conducted under a research permit granted by the Department of Environment, Land, Water and
406 Planning (Permit No. 10008063).

407 **Conflict of interest:** The authors declare that they have no known competing financial interests or
408 personal relationships that could have appeared to influence the work reported in this paper.

409 **Ethics approval:** Not applicable.

410 **Consent to participate:** Not applicable.

411 **Consent for publication:** Not applicable.

412 **Availability of data and material:** The data that support the findings of this study are available from the
413 corresponding author upon reasonable request.

414 **Code availability:** All code for analysing the data associated with the submission/ article is available from
415 the corresponding author upon reasonable request.

416 **Authors' contributions:** SF, JG, CW and JC conceived the study and developed the methodology. SF and
417 JG conducted the fieldwork. SF, JG and CW analysed the data. SF wrote the main manuscript text; all other
418 authors reviewed the manuscript and provided editorial advice.

419

- 421 1. Petit, R.J. and A. Hampe, *Some evolutionary consequences of being a tree*. *Annu. Rev. Ecol. Evol.*
422 *Syst.*, 2006. **37**: p. 187-214.
- 423 2. Chapin III, F.S., E. Schulze, and H.A. Mooney, *The ecology and economics of storage in plants*.
424 *Annual Review of Ecology and Systematics*, 1990. **21**(1): p. 423-447.
- 425 3. Davidson, N.C., *How much wetland has the world lost? Long-term and recent trends in global*
426 *wetland area*. *Marine and Freshwater Research*, 2014. **65**(10): p. 934-941.
- 427 4. Rodríguez-González, P.M., et al., *Subsidy or stress? Tree structure and growth in wetland forests*
428 *along a hydrological gradient in Southern Europe*. *Forest Ecology and Management*, 2010.
429 **259**(10): p. 2015-2025.
- 430 5. Magonigal, J.P., et al., *Aboveground production in southeastern floodplain forests: a test of the*
431 *subsidy–stress hypothesis*. *Ecology*, 1997. **78**(2): p. 370-384.
- 432 6. Kozłowski, T.T., *Physiological-ecological impacts of flooding on riparian forest ecosystems*.
433 *Wetlands*, 2002. **22**(3): p. 550-561.
- 434 7. Catford, J.A. and R. Jansson, *Drowned, buried and carried away: effects of plant traits on the*
435 *distribution of native and alien species in riparian ecosystems*. *New Phytologist*, 2014. **204**(1): p.
436 19-36.
- 437 8. Vesk, P.A. and M. Westoby, *Sprouting ability across diverse disturbances and vegetation types*
438 *worldwide*. *Journal of Ecology*, 2004. **92**(2): p. 310-320.
- 439 9. Ellis, M.V., J.E. Taylor, and L. Rayner, *Growth characteristics of Eucalyptus camaldulensis trees*
440 *differ between adjacent regulated and unregulated rivers in semi-arid temperate woodlands*.
441 *Forest Ecology and Management*, 2017. **398**: p. 1-9.
- 442 10. Jensen, A., K. Walker, and D. Paton, *Using phenology of eucalypts to determine environmental*
443 *watering regimes for the River Murray floodplain South Australia*, in *Proceedings of the 5th*
444 *Australian Stream Management Conference 2007*, Charles Sturt Univeristy, New South Wales.
- 445 11. Zizka, A., N. Govender, and S.I. Higgins, *How to tell a shrub from a tree: A life-history perspective*
446 *from a South African savanna*. *Austral Ecology*, 2014. **39**(7): p. 767-778.
- 447 12. Woolfrey, A.R. and P.G. Ladd, *Habitat preference and reproductive traits of a major Australian*
448 *riparian tree species (Casuarina cunninghamiana)*. *Australian Journal of Botany*, 2001. **49**(6): p.
449 705-715.
- 450 13. Iwanaga, F. and F. Yamamoto, *Effects of flooding depth on growth, morphology and*
451 *photosynthesis in Alnus japonica species*. *New Forests*, 2008. **35**(1): p. 1-14.
- 452 14. Raulings, E.J., et al., *The importance of water regimes operating at small spatial scales for the*
453 *diversity and structure of wetland vegetation*. *Freshwater Biology*, 2010. **55**(3): p. 701-715.
- 454 15. Dawson, S.K., et al., *Plant traits of propagule banks and standing vegetation reveal flooding*
455 *alleviates impacts of agriculture on wetland restoration*. *Journal of Applied Ecology*, 2017. **54**(6):
456 p. 1907-1918.
- 457 16. Taylor, J.E., et al., *Variability in allometric relationships for temperate woodland Eucalyptus*
458 *trees*. *Forest Ecology and Management*, 2016. **360**: p. 122-132.
- 459 17. Pausas, J.G. and J.E. Keeley, *Evolutionary ecology of resprouting and seeding in fire-prone*
460 *ecosystems*. *New Phytologist*, 2014. **204**(1): p. 55-65.
- 461 18. Bellingham, P., T. Kohyama, and S.-i. Aiba, *The effects of a typhoon on Japanese warm*
462 *temperate rainforests*. *Ecological Research*, 1996. **11**(3): p. 229-247.
- 463 19. Nzunda, E.F., M.E. Griffiths, and M.J.J.J.o.t.e. Lawes, *Resprouting versus turning up of leaning*
464 *trees in a subtropical coastal dune forest in South Africa*. *Journal of Tropical Ecology*, 2007. **23**(3):
465 p. 289-296.

- 466 20. Stokes, A., et al., *Multi-stemming and mechanical traits ensure persistence of subalpine woody*
467 *plants exposed to a disturbance gradient*. Journal of Vegetation Science, 2012. **23**(2): p. 325-338.
- 468 21. Salter, J., et al., *Understanding the potential effects of water regime and salinity on recruitment*
469 *of Melaleuca ericifolia Sm*. Aquatic Botany, 2010. **92**(3): p. 200-206.
- 470 22. Bellingham, P.J. and A.D. Sparrow, *Resprouting as a life history strategy in woody plant*
471 *communities*. Oikos, 2000. **89**(2): p. 409-416.
- 472 23. Bond, W.J. and J.J. Midgley, *Ecology of sprouting in woody plants: the persistence niche*. Trends
473 in Ecology & Evolution, 2001. **16**(1): p. 45-51.
- 474 24. Deiller, A.-F., J.-M.N. Walter, and M. Trémolières, *Regeneration strategies in a temperate*
475 *hardwood floodplain forest of the Upper Rhine: sexual versus vegetative reproduction of woody*
476 *species*. Forest Ecology and Management, 2003. **180**(1): p. 215-225.
- 477 25. Turner, V., *Action statement: Sedge-rich Eucalyptis camphora Swamp*. Report to the Department
478 of Sustainability and Environment, Aurther Rylah Institute, Melbourne, 2003.
- 479 26. McMahon, A. and D. Franklin, *The significance of mountain swamp gum for helmeted*
480 *honeyeater populations in the Yarra Valley*. Victorian Naturalist, 1993. **110**(6): p. 230-37.
- 481 27. Craigie, N., S. Brizga, and P. Condina, *Assessment of proposed works to ameliorate the effect of*
482 *hydrological processes on vegetation dieback at Cockatoo Creek Swamp, Yellingbo Reserve*. A
483 report to Parks Victoria. Neil M Craigie Pty Ltd, Melbourne, 1998.
- 484 28. Greet, J., *The marked flooding tolerance of seedlings of a threatened swamp gum: implications*
485 *for the restoration of critical wetland forests*. Australian Journal of Botany, 2015. **63**(8): p. 669-
486 678.
- 487 29. Zacks, G., et al., *The flooding tolerance of two critical habitat-forming wetland shrubs,*
488 *Leptospermum lanigerum and Melaleuca squarrosa, at different life history stages*. Australian
489 Journal of Botany, 2019. **66**(7): p. 500-510.
- 490 30. Cunningham, S.C., et al., *Quantitative assessment of stand condition and its relationship to*
491 *physiological stress in stands of Eucalyptus camaldulensis (Myrtaceae)*. Australian Journal of
492 Botany, 2007. **55**(7): p. 692-699.
- 493 31. Souter, N., et al., *Method manual for the visual assessment of Lower River Murray floodplain*
494 *trees. River red gum (Eucalyptus camaldulensis)*. DWLBC Report 2009, 2009. **25**.
- 495 32. Greet, J., S. Fischer, and K. Russell, *Longer duration flooding reduces the growth and sexual*
496 *reproductive efforts of a keystone wetland tree species*. Wetlands Ecology and Management,
497 2020. **28**(4): p. 655-666.
- 498 33. Zeileis, A., et al., *Beta regression in R*. 2010. **34**(2): p. 1-24.
- 499 34. Venables, W. and B. Ripley, *Modern applied statistics 4th ed*. 2002, New York: Springer.
- 500 35. Mac Nally, R. and C.J. Walsh, *Hierarchical partitioning public-domain software*. Biodiversity &
501 Conservation, 2004. **13**(3): p. 659.
- 502 36. Chevan, A. and M. Sutherland, *Hierarchical partitioning*. The American Statistician, 1991. **45**(2):
503 p. 90-96.
- 504 37. Mac Nally, R., *Multiple regression and inference in ecology and conservation biology: further*
505 *comments on identifying important predictor variables*. Biodiversity & Conservation, 2002. **11**(8):
506 p. 1397-1401.
- 507 38. Signorell, A., et al., *DescTools: Tools for descriptive statistics. R package version 0.99*. 28. 2019.
- 508 39. R Development Core Team, *R: A language and environment for statistical computing. R*
509 *Foundation for Statistical Computing*. 2018: Vienna, Austria.
- 510 40. Parolin, P.d., et al., *Central Amazonian floodplain forests: tree adaptations in a pulsing system*.
511 The Botanical Review, 2004. **70**(3): p. 357-380.

- 512 41. Merritt, D.M., et al., *Theory, methods and tools for determining environmental flows for riparian*
513 *vegetation: riparian vegetation-flow response guilds*. *Freshwater Biology*, 2010. **55**(1): p. 206-
514 225.
- 515 42. Ernst, K.A., J.R. Brooks, and Management, *Prolonged flooding decreased stem density, tree size*
516 *and shifted composition towards clonal species in a central Florida hardwood swamp*. *Forest*
517 *Ecology*, 2003. **173**(1-3): p. 261-279.
- 518 43. Chong, C., et al., *Sprouting and genetic structure vary with flood disturbance in the tropical*
519 *riverine paperbark tree, Melaleuca leucadendra (Myrtaceae)*. *American Journal of Botany*, 2013.
520 **100**(11): p. 2250-2260.
- 521 44. Van Bloem, S.J., P.G. Murphy, and A.E. Lugo, *Subtropical dry forest trees with no apparent*
522 *damage sprout following a hurricane*. *Tropical Ecology*, 2003. **44**(2): p. 137-146.
- 523 45. Meier, A.R., M.R. Saunders, and C.H. Michler, *Epicormic buds in trees: a review of bud*
524 *establishment, development and dormancy release*. *Tree Physiology*, 2012. **32**(5): p. 565-584.
- 525 46. Read, J. and A. Stokes, *Plant biomechanics in an ecological context*. *American Journal of Botany*,
526 2006. **93**(10): p. 1546-1565.
- 527 47. Pearce, J., *Mountain Swamp Gum Eucalyptus camphora at Yellingbo State Nature Reserve:*
528 *Habitat use by the endangered Helmeted Honeyeater Lichenostomus melanops cassidix and*
529 *implications for management*. *Victorian Naturalist*, 2000. **117**(3): p. 84-92.
- 530 48. Lawson, J.R., K.A. Fryirs, and M.R. Leishman, *Hydrological conditions explain variation in wood*
531 *density in riparian plants of south-eastern Australia*. *Journal of Ecology*, 2015. **103**(4): p. 945-
532 956.
- 533 49. Loehle, C., *Biomechanical constraints on tree architecture*. *Trees*, 2016. **30**(6): p. 2061-2070.
- 534 50. Shibata, R., et al., *Relationships between resprouting ability, species traits and resource*
535 *allocation patterns in woody species in a temperate forest*. *Functional Ecology*, 2016. **30**(7): p.
536 1205-1215.
- 537 51. Obeso, J.R., *The costs of reproduction in plants*. *New Phytologist*, 2002. **155**(3): p. 321-348.
- 538 52. Clarke, P.J., et al., *Resprouting as a key functional trait: how buds, protection and resources drive*
539 *persistence after fire*. *New Phytologist*, 2013. **197**(1): p. 19-35.
- 540 53. Mukassabi, T.A., et al., *Scots pine seed dynamics on a waterlogged site*. *Trees*, 2012. **26**(4): p.
541 1305-1315.
- 542 54. Minor, D.M. and R.K. Kobe, *Fruit production is influenced by tree size and size-asymmetric*
543 *crowding in a wet tropical forest*. *Ecology and Evolution*, 2019. **9**(3): p. 1458-1472.
- 544 55. Thomson, F.J., et al., *Seed dispersal distance is more strongly correlated with plant height than*
545 *with seed mass*. *Journal of Ecology*, 2011. **99**(6): p. 1299-1307.
- 546 56. Møller, A. and M.D. Jennions, *How much variance can be explained by ecologists and*
547 *evolutionary biologists?* *Oekologia*, 2002. **132**(4): p. 492-500.
- 548 57. Bannister, J.R., et al., *Importance of structure for species richness and tree species regeneration*
549 *niches in old-growth Patagonian swamp forests*. *Forest Ecology*, 2017. **401**: p. 33-44.

550 **Tables**

551

552 *Table 1 measured morphology and reproduction variables and distribution for model fitting*

Tree measurements	Unit	Distribution
<i>Morphology variables</i>		
<i>Main stem DBH</i>	cm	Gaussian
<i>Height</i>	m	Gaussian
<i>Crown width</i>	m	Gaussian
<i>Crown extent</i>	%	Beta
<i>Number of stems</i>	integer	Poisson
<i>Leaning</i>	°	Beta
<i>Reproductive strategy variables</i>		
<i>Sexual reproduction</i>	Score 0-3	Binominal
<i>Epicormic growth</i>	Score 0-3	Binominal

553

554 Table 2 Explained variance of models of growth-form and reproductive strategy variables as a function of
 555 flood frequency and duration. Explained variance (in bold) is expressed as R^2 or pseudo- R^2 as
 556 appropriate. For each predictor variable, its proportional independent contribution is shown, and, if its
 557 total contribution to explained variance (i.e. proportion explained $\times R^2$) > 0.05 , the direction of the effect
 558 (dir) is indicated as positive, "+", or negative, "-". Variables that independently explained a larger
 559 proportion of variance than could be explained by chance are marked with an asterisk. Sample sizes were
 560 $n = 129$ for *E. camphora*, $n = 75$ for *L. lanigerum*, $n = 74$ for *M. squarrosa* for all response variables except
 561 for plant height for which $n = 108$ for *E. camphora* and $n = 74$ for *L. lanigerum*. DBH = Diameter at breast
 562 height. dir = direction of effect. var = proportion of explained variance (bold) and contribution to
 563 explained variance, respectively.

	<i>E. camphora</i>		<i>L. lanigerum</i>		<i>M. squarrosa</i>	
	dir	var	dir	var	dir	var
Morphology variables						
<i>main stem DBH</i>						
R^2		0.07				
Frequency	-	0.75*				
Duration		0.25				
<i>Height</i>						
R^2		0.13			0.05	
Frequency	-	0.90*			0.17	
Duration		0.10			0.83	
<i>Crown width</i>						
R^2			0.05		0.05	
Frequency			0.80		0.83	
Duration			0.20		0.17	
<i>Crown extent</i>						
Pseudo- R^2						
Frequency						
Duration						
<i>Number of stems</i>						
R^2		0.10	0.10		0.27	

Frequency	+	0.90*	0.03	+	0.47*
Duration		0.10	+ 0.97*	+	0.53*
<i>Leaning</i>					
Pseudo-R ²		0.11	0.13		0.20
Frequency	+	0.57*	+ 0.81*		0.20
Duration	+	0.43*	0.19	+	0.80*
<i>Reproductive strategy</i>					
<i>variables</i>					
<i>Sexual reproduction</i>					
Pseudo-R ²		0.13			
Frequency	-	0.90*			
Duration		0.10			
<i>Epicormic growth</i>					
Pseudo-R ²		0.07			0.07
Frequency	+	0.83*			0.04
Duration		0.17		+	0.96*

565 *Table 3 Explained variance of models of reproductive strategy variables as a function of growth-form*
566 *variables. Explained variance (in bold) is expressed as pseudo-R². For each predictor variable, its*
567 *proportional independent contribution is shown, and, if its total contribution to explained variance (i.e.*
568 *proportion explained x R²) > 0.05, the direction of the effect (dir) is indicated as positive, “+”, or*
569 *negative,” – “. Variables that independently explained a larger proportion of variance than could be*
570 *explained by chance are marked with an asterisk. Sample sizes were n = 111 for E. camphora, n = 76 for*
571 *L. lanigerum and n = 77 for M. squarrosa. DBH = Diameter at breast height. var = proportion of explained*
572 *variance (bold) and contribution to explained variance, respectively.*

	<i>E. camphora</i>		<i>L. leptospermum</i>		<i>M. squarrosa</i>	
	dir	var	dir	var	dir	Var
<i>Sexual reproduction</i>						
Pseudo R ²		0.18		0.16		0.28
Main Stem DBH	+	0.64*	+	0.36*		0.13
Height	+	0.57	-	0.53	-	0.23*
Crown Width		0.13		0.10	+	0.92
Stem Number	-	0.70	-	0.41		0.10
Leaning	+	0.26	-	0.32*	-	0.82
Crown extent	+	0.79		0.12	+	0.36*
<i>Epicormic growth</i>						
Pseudo R ²		0.25		0.13		0.16
Main Stem	-	0.63		0.21	+	0.46*
Height	-	0.88		0.12		0.22
Crown Width		0.14		0.11	+	0.29*
Stem Number	+	0.56	+	0.70		0.17
Leaning	+	0.76*		0.31		0.19
Crown extent	-	0.21	-	0.47*	-	0.33

574 **Figure legends**

575 **Fig. 1** Hypothetical gradient in morphology and reproductive strategy of woody riparian plants in response
576 to flood disturbance. Individuals that grow further from a channel or in higher elevations (left hand side)
577 will experience less disturbance, i.e. shorter duration or less frequent flooding, which should hypothetically
578 result in plants that are taller, single-stemmed and largely exhibit sexual or seed-based reproduction
579 (symbolised by presence of flowers). In contrast, individuals that experience more disturbance (right hand
580 side) will be more likely to have leaning stems, be shorter, multi-stemmed and reliant on vegetative
581 reproduction (symbolised by epicormic resprouts).

582

583 **Fig. 2** Map of all surveyed individuals of the three studied species within the Yellingbo Nature
584 Conservation Reserve (green polygon). Shading represents flooding gradient categories used for sample
585 point stratification (with grey indicating non-flood-prone areas and blues indicating flood-prone areas
586 with darker blues representing higher flood-proneness).

587

588 **Fig. 3** Boxplots of main stem DBH (a), plant height (b), crown width (c), crown extent (d), stem number
589 (e) and stem leaning (f) for surveyed plants of the three studied species. Coloured points indicate raw
590 data ($n = 129$ for *E. camphora*, $n = 75$ for *L. lanigerum*, $n = 74$ for *M. squarrosa* for all variables except for
591 plant height for which $n = 108$ for *E. camphora* and $n = 74$ for *L. lanigerum*). DBH = diameter at breast
592 height. *E. cam* = *E. camphora*, *L. lan* = *L. lanigerum*, *M. squ* = *M. squarosa*.

593

594 **Fig. 4** Relationships of flood duration and frequency and measured morphology variables, sexual
595 reproduction and epicormic growth for *E. camphora*, *L. lanigerum* and *M. squarrosa*. Only relationships
596 from models with R^2 or pseudo $R^2 > 0.05$ and for predictor variables with a significant independent
597 contribution to the overall explained variance > 0.30 are shown. Note that plots show untransformed
598 values for flood duration and frequency whereas statistical modelling was undertaken using log
599 transformed values. Points indicate raw data ($n = 129$ for *E. camphora*, $n = 75$ for *L. lanigerum*, $n = 74$ for
600 *M. squarrosa*). Frequency (events/yr) = mean number of flooding events per year; Duration (days) = mean
601 flooding event duration; Sexual reproduction = score for sexual reproduction; Epicormic growth = score for
602 epicormic growth.

603 **Fig. 5** Relationships between morphology variables and sexual reproduction and epicormic growth for *E.*
604 *camphora*, *L. leptospermum* and *M. squarrosa*. Only relationships for predictor variables with a
605 significant independent contribution > 0.30 to the explained variance are shown. Points indicate raw
606 data ($n = 111$ for *E. camphora*, $n = 76$ for *L. lanigerum*, $n = 77$ for *M. squarrosa*). DBH = Diameter at
607 breast height.

Figures

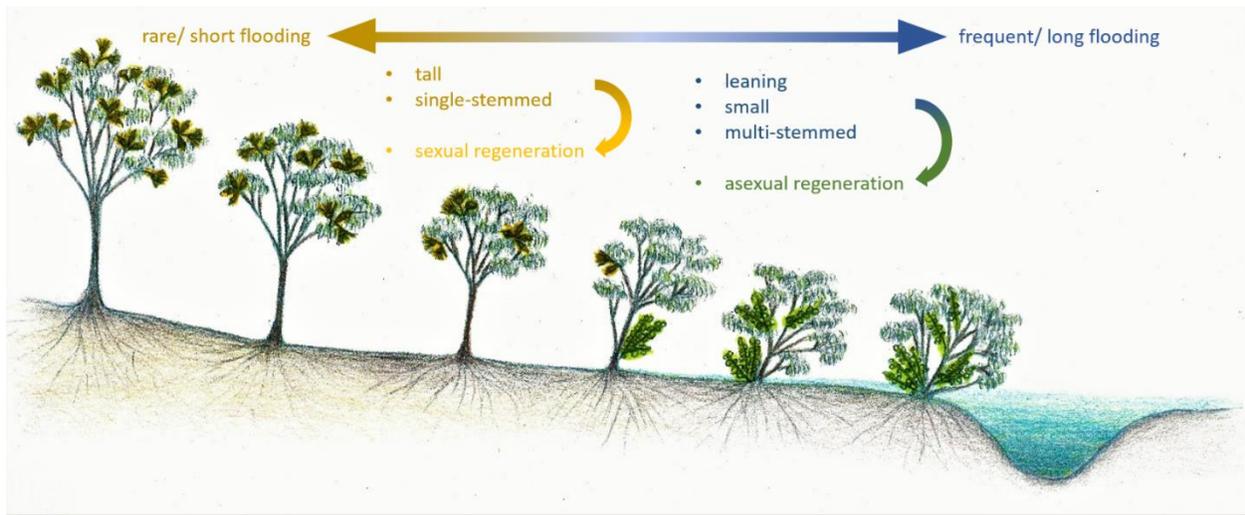


Fig. 1

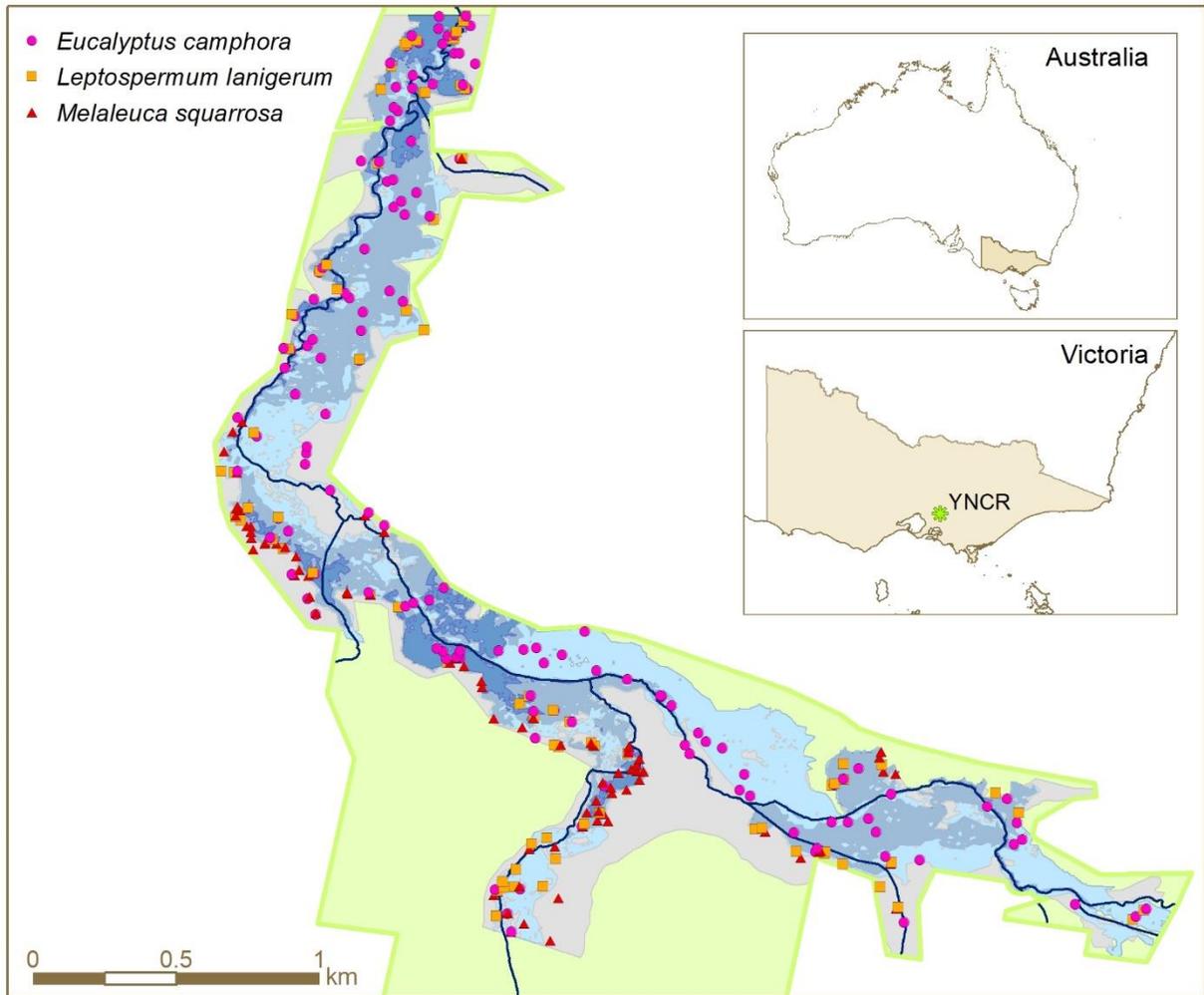


Fig. 2

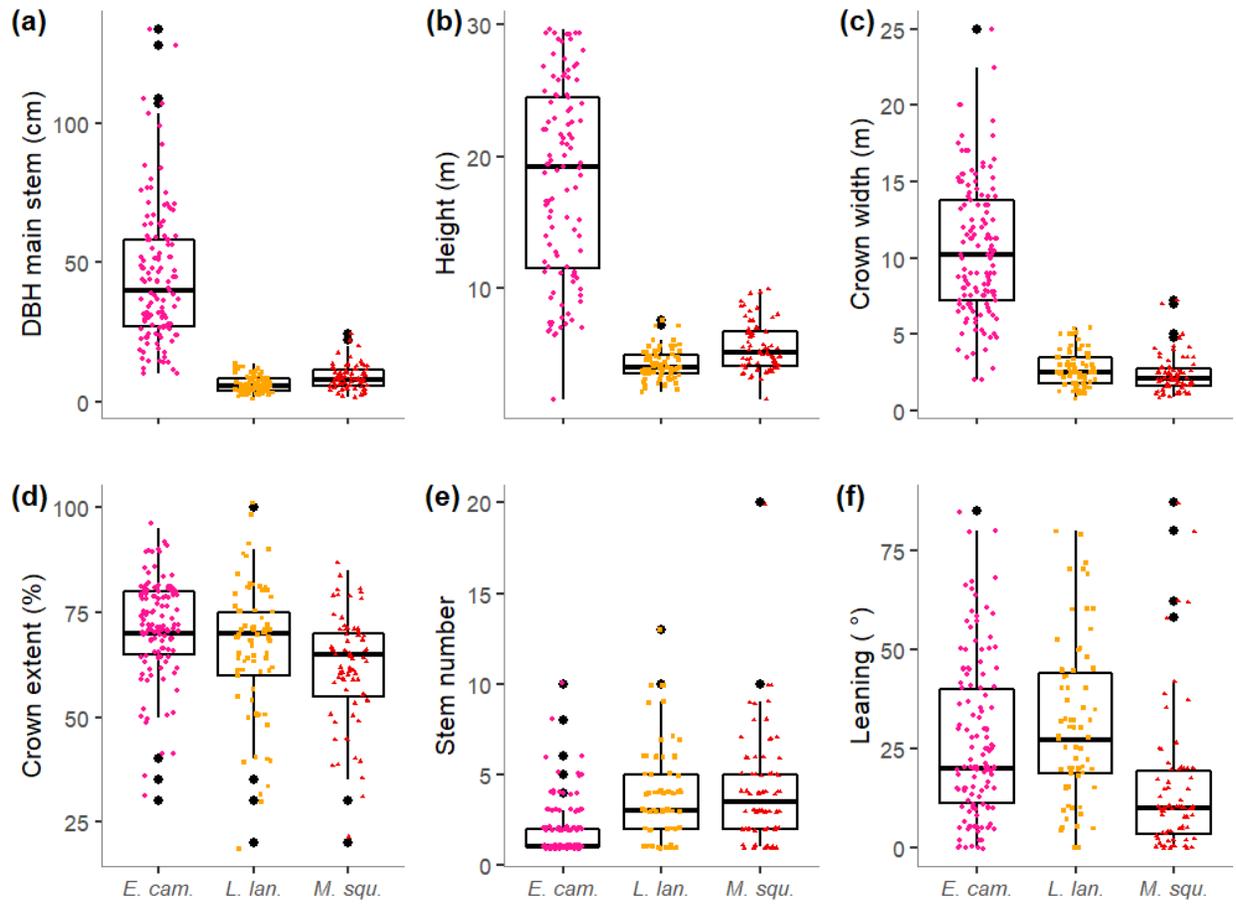


Fig. 3

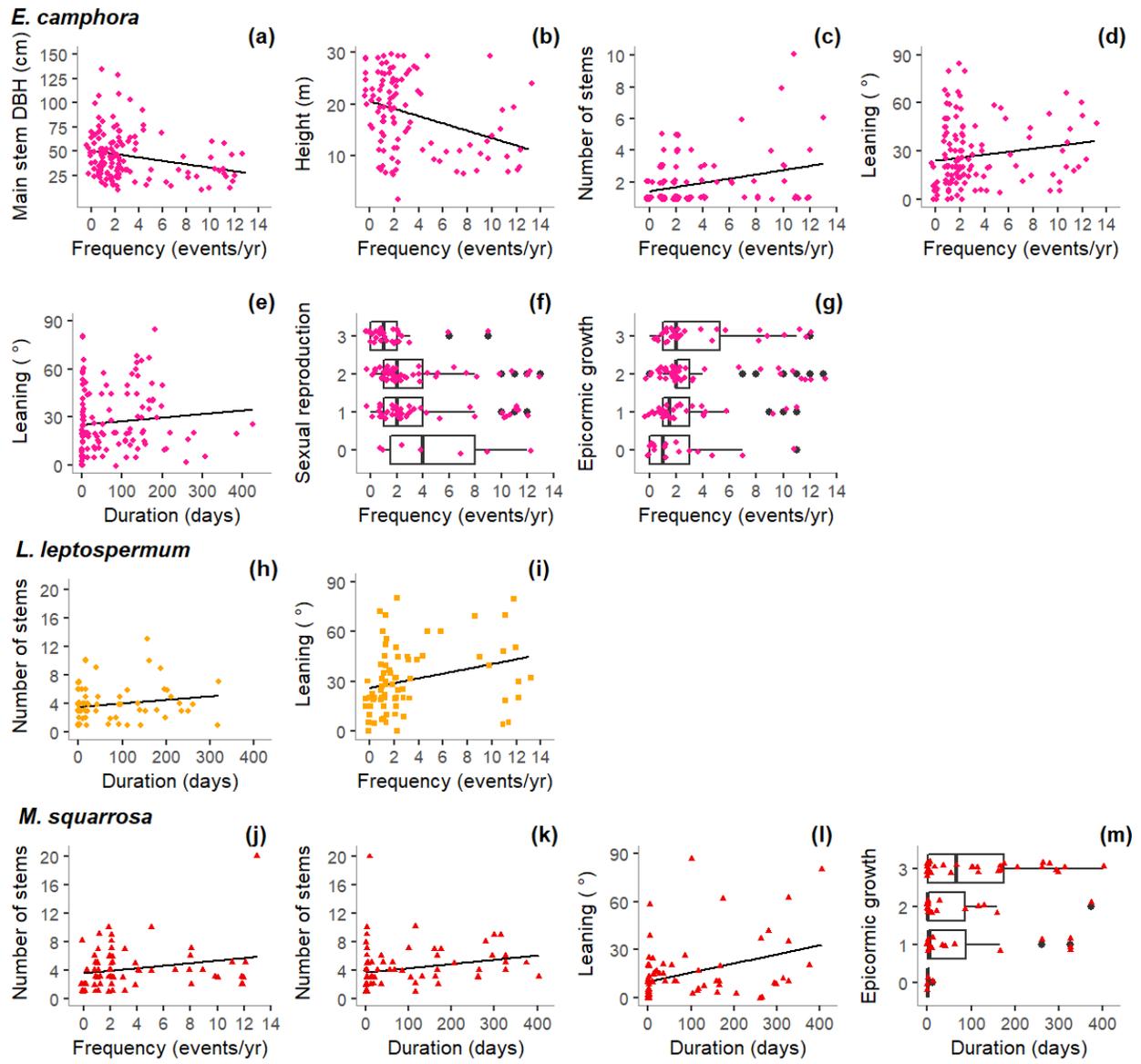


Fig. 4

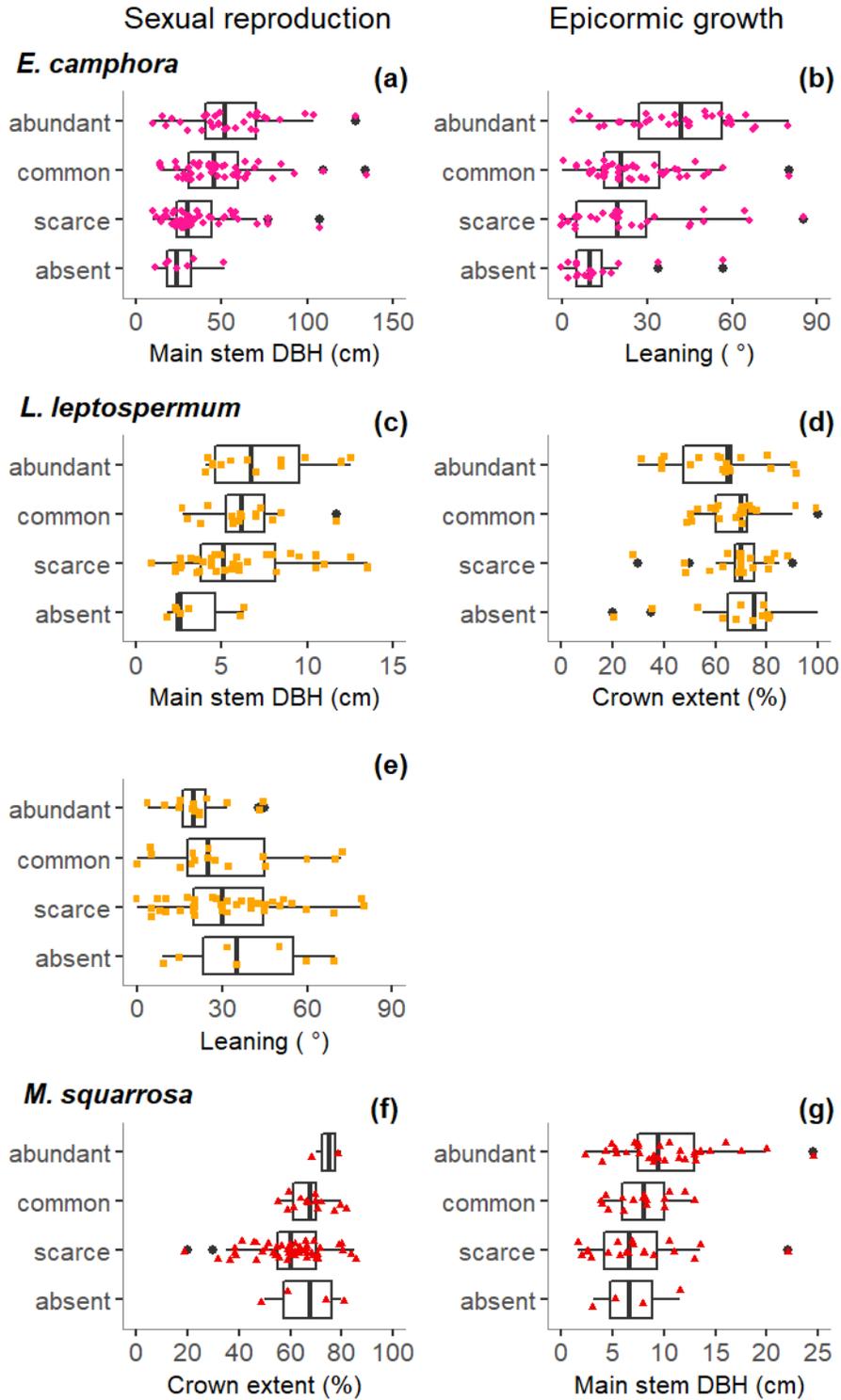


Fig. 5

Figures

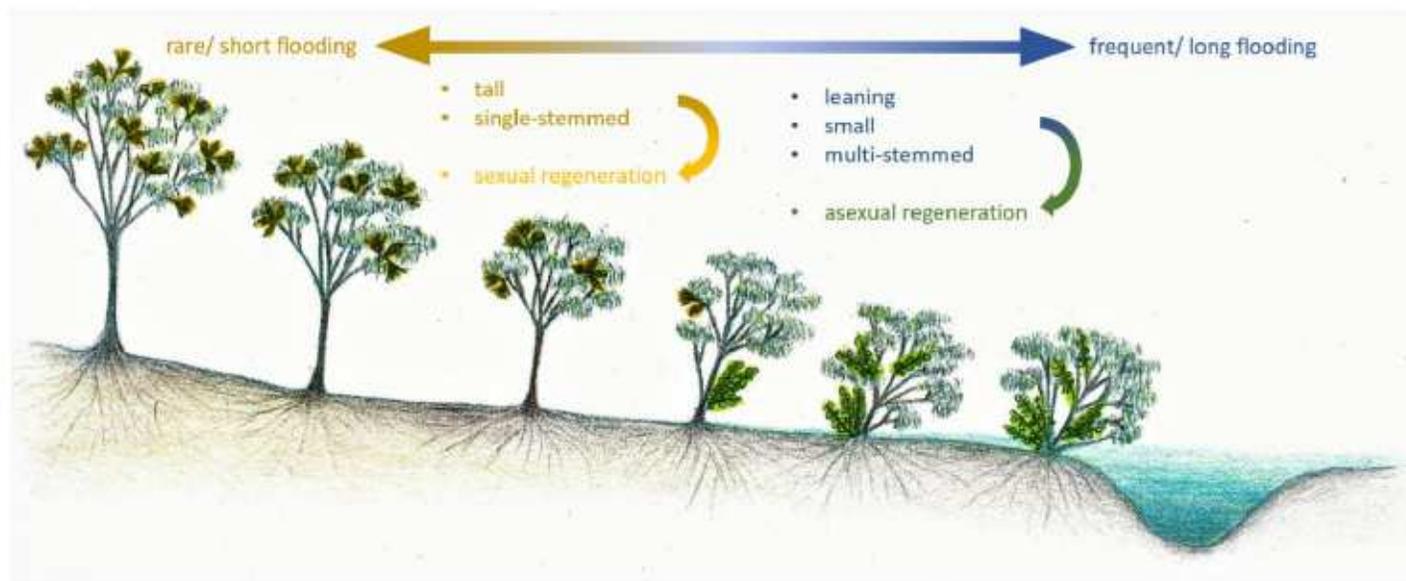


Figure 1

Hypothetical gradient in morphology and reproductive strategy of woody riparian plants in response to flood disturbance. Individuals that grow further from a channel or in higher elevations (left hand side) will experience less disturbance, i.e. shorter duration or less frequent flooding, which should hypothetically result in plants that are taller, single-stemmed and largely exhibit sexual or seed-based reproduction (symbolised by presence of flowers). In contrast, individuals that experience more disturbance (right hand side) will be more likely to have leaning stems, be shorter, multi-stemmed and reliant on vegetative reproduction (symbolised by epicormic resprouts).

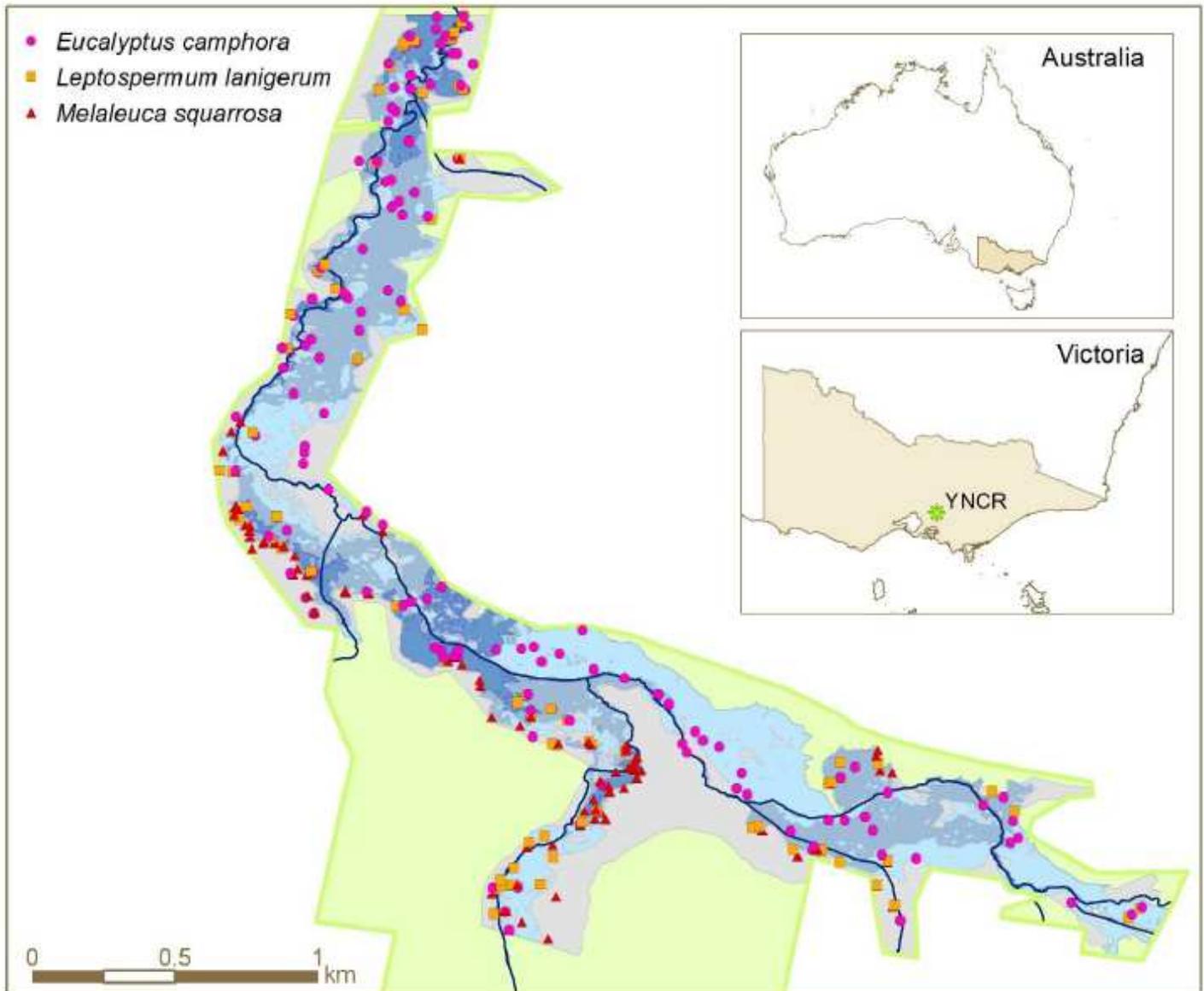


Figure 2

Map of all surveyed individuals of the three studied species within the Yellingbo Nature Conservation Reserve (green polygon). Shading represents flooding gradient categories used for sample point stratification (with grey indicating non-flood-prone areas and blues indicating flood-prone areas with darker blues representing higher flood-proneness). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

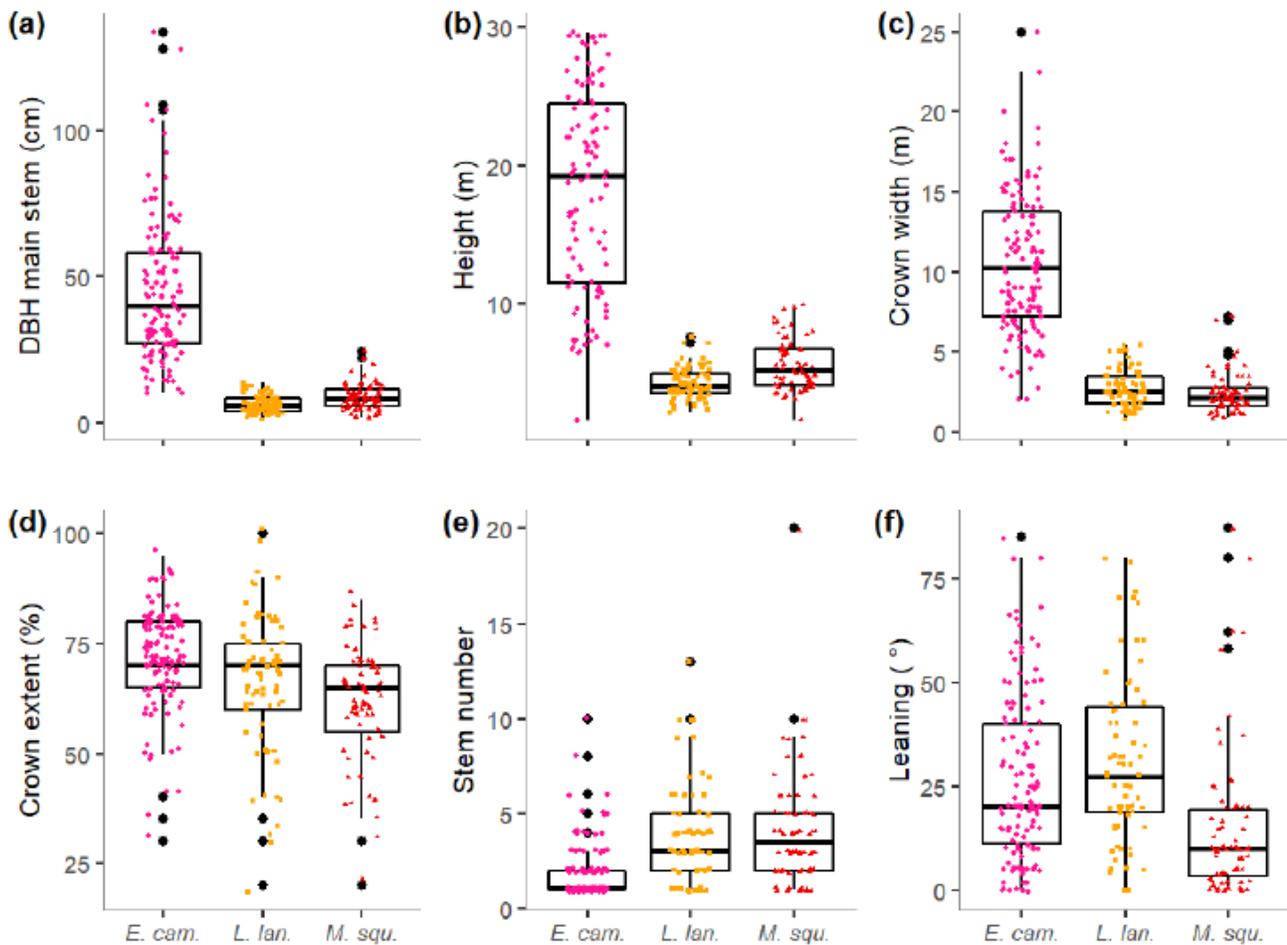


Figure 3

Boxplots of main stem DBH (a), plant height (b), crown width (c), crown extent (d), stem number (e) and stem leaning (f) for surveyed plants of the three studied species. Coloured points indicate raw data ($n = 129$ for *E. camphora*, $n = 75$ for *L. lanigerum*, $n = 74$ for *M. squarrosa* for all variables except for plant height for which $n = 108$ for *E. camphora* and $n = 74$ for *L. lanigerum*). DBH = diameter at breast height. *E. cam* = *E. camphora*, *L. lan* = *L. lanigerum*, *M. squ* = *M. squarosa*.

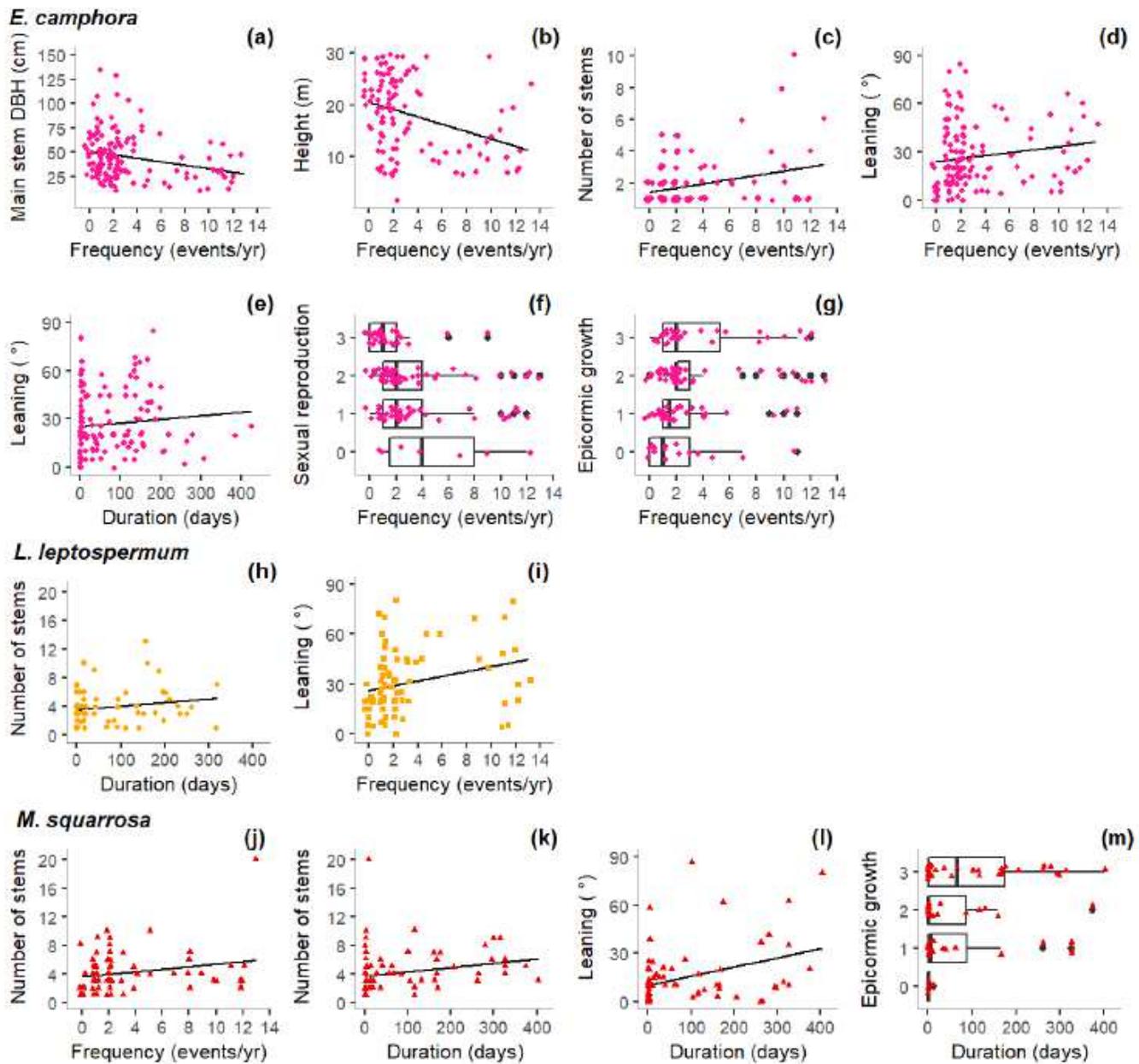


Figure 4

Relationships of flood duration and frequency and measured morphology variables, sexual reproduction and epicormic growth for *E. camphora*, *L. lanigerum* and *M. squarrosa*. Only relationships from models with R^2 or pseudo $R^2 > 0.05$ and for predictor variables with a significant independent contribution to the overall explained variance > 0.30 are shown. Note that plots show untransformed values for flood duration and frequency whereas statistical modelling was undertaken using log transformed values. Points indicate raw data ($n = 129$ for *E. camphora*, $n = 75$ for *L. lanigerum*, $n = 74$ for *M. squarrosa*). Frequency (events/yr) = mean number of flooding events per year; Duration (days) = mean flooding event duration; Sexual reproduction = score for sexual reproduction; Epicormic growth = score for epicormic growth.

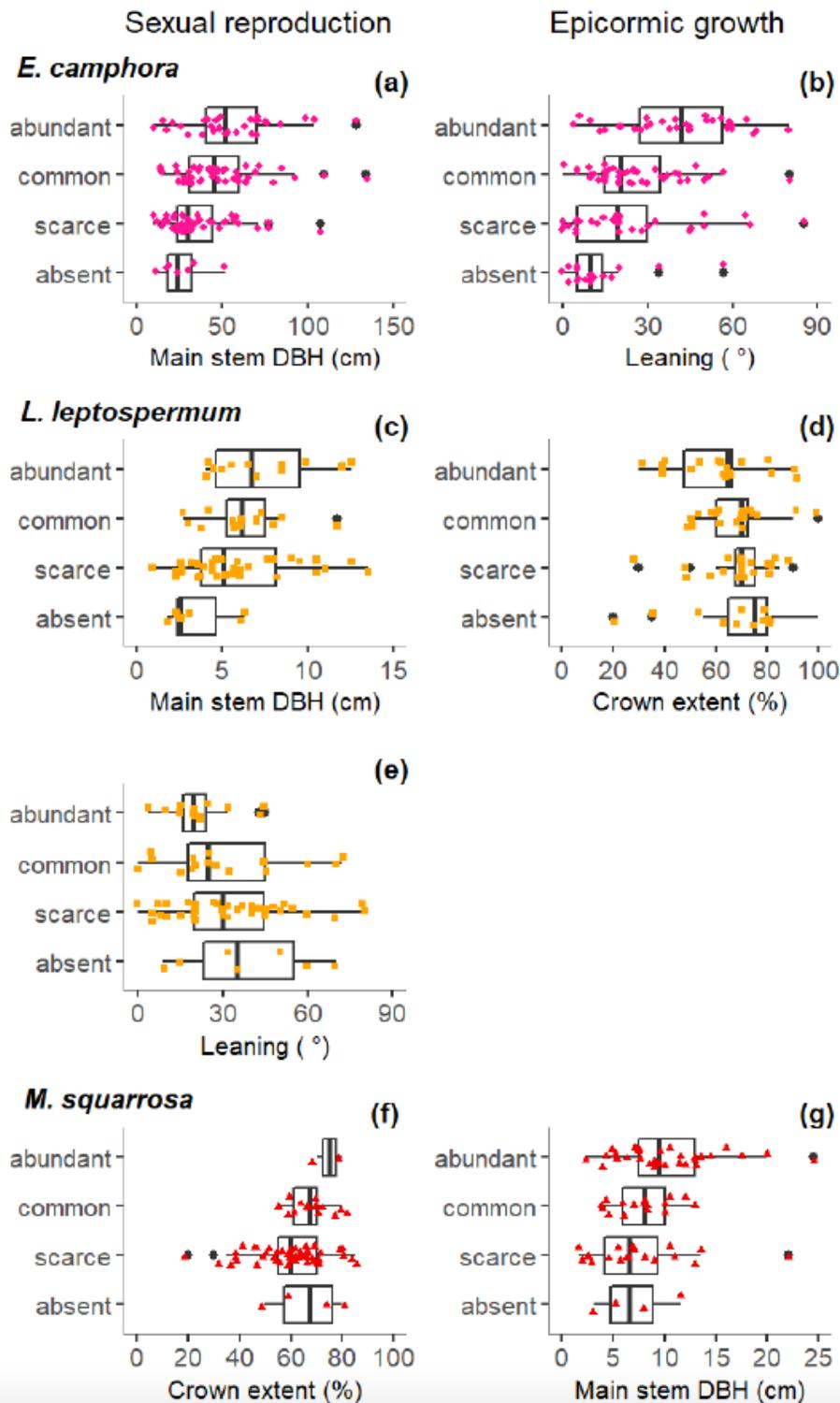


Figure 5

Relationships between morphology variables and sexual reproduction and epicormic growth for *E. camphora*, *L. leptospermum* and *M. squarrosa*. Only relationships for predictor variables with a significant independent contribution > 0.30 to the explained variance are shown. Points indicate raw data ($n = 111$ for *E. camphora*, $n = 76$ for *L. lanigerum*, $n = 77$ for *M. squarrosa*). DBH = Diameter at breast height.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SRFloodsAlterTreeMorphReproESM09042021.pdf](#)