

Title page

Title: Predicting the occurrence of riparian woody species to inform environmental water policies in an Australian tropical river

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Abstract

1. River flows are commonly altered by water resource development, with changes to the natural flow regime potentially impacting riparian vegetation. Increasingly, water resource managers seek to design policy to maintain healthy riparian ecosystems. Models that make explicit the relationship between hydrological variables and vegetation can be used by managers to assess vegetation response under different water management scenarios.
2. We determined the potential impact of water extraction on the spatial distribution of woody riparian plant species in the lower Fitzroy River, in north-western Australia, an area under pressure to increase water resource development. We undertook a plant survey and developed and applied a joint species distribution model (JDSM) to determine the likelihood of occurrence for 26 woody riparian plant species, mapped species occurrence and assessed the change in species distribution under two water-take scenarios.
3. We found that the duration of inundation from flood flows was a strong predictor of species occurrence in our JDSM. We identified species associated with wetter environments, as indicated by their effect size for the inundation metric. Under the 300 gigalitre (GL) water-take scenario we found little change (<2 %) in species occurrence, but under the 600 GL scenario a decline between 5 and 7.4 % was predicted for eight species associated with wetter habitats. This decline was generally confined to a localised area.
4. Our approach highlights the usefulness of predictive modelling to identify species most likely to be impacted by water-take, and the benefit of linking modelling to spatial mapping because it can highlight areas where change is likely to occur. This information can assist management to protect ecologically and culturally important species.

Introduction

Freshwater habitats, including rivers and their associated riparian zones, are some of the most threatened ecosystems on earth (Flitcroft, Cooperman, Harrison, Juffe-Bignoli, & Boon, 2019; Vörösmarty et al., 2010). A large proportion of the world's rivers are regulated by dams or other infrastructure that alters flow, with 44 to 63 % of long rivers no longer free-flowing (Grill et al., 2019). Riparian zones can suffer significant impacts from altered hydrology because the dynamics of these systems are governed primarily by flow regime, with the timing and duration of flooding driving the distribution of riparian biota, including vegetation species assemblages (Lawson, Fryirs, Lenz, & Leishman, 2015; White & Stromberg, 2011). Changes in flow that result in altered distributions and assemblage structure of riparian plants can have many secondary effects on the ecosystem, including altered river geomorphology (Hubble, Docker, & Rutherford, 2010; Naiman, Decamps, & Pollock, 1993), reduced inputs to the aquatic food web (Pusey & Arthington, 2003), and reduced habitat availability for terrestrial animals (Blakey, Kingsford, Law, & Stoklosa, 2017; Skroblin & Legge, 2012). The broad influence of riparian vegetation is a key reason why maintaining healthy riparian vegetation communities is a common conservation concern (Bennett, Nimmo, & Radford, 2014; Pusey & Arthington, 2003).

Increasingly, water resource managers are aiming to manage flow regimes to maintain healthy riparian vegetation and protect vital ecosystem processes and the people who rely on them (Arthington et al., 2018; Crow, Tipa, Booker, & Nelson, 2018; Magdaleno, 2018). However, determining management strategies to achieve these goals can be difficult because managers must be able to predict the outcomes of management options for complex and dynamic ecosystems. For most natural resource and ecosystem management, these predictions are based on the managers' experiences and opinions which can be inconsistent, subject to many implicit biases (Klayman, Busemeyer, Hastie, & Medin, 1995; Maqsood, Finegan, & Walker, 2004), and difficult to learn from and pass on to future managers.

Potential biases can be reduced and made explicit through the use of predictive models, such as species distribution models, which predict the occurrence of species based on the known occurrence and site conditions (Guisan et al., 2013). Species distribution models are often used in conservation to assess the likely impact of a management action on a species or community (Guisan et al., 2013), and are beginning to be used to predict changes in wetland and riparian species occurrence under different water regimes (Moxham, Kenny, Beesley, & Gwinn, 2019). A modelling approach makes a direct link between environmental variables and species occurrence, to effectively inform the decision-making process.

Modelling of riparian vegetation to support water management decisions requires the use of hydrological variables that are ecologically appropriate. Flood flows are important drivers of the distribution of riparian species across landscapes, providing important functions such as the distribution of seed (Nilsson, Brown, Jansson, & Merritt, 2010) and replenishment of soil water stores and alluvial aquifers (Doble, Crosbie, Smerdon, Peeters, & Cook, 2012), which can be important water sources for plants in seasonally dry environments (Lamontagne, Cook, O'Grady, & Eamus, 2005). Flood flows also help maintain riparian species that are adapted to this environmental stressor (Rivaes et al., 2015), with species assemblage reflecting tolerance of inundation (Todd et al., 2010; Zhang, Yin, Jiang, & Wang, 2012). Many riparian species can withstand long periods of inundation, with physiological adaptations such as aerenchyma tissue and developing extensive adventitious roots (Argus, Colmer, & Grierson, 2015; Catford & Jansson, 2014). Other species are less tolerant of inundation and the distribution of species along a lateral gradient often reflects the hydrological regime (Jansson et al. 2019). Flood flow, and in particular the duration of inundation, is a useful hydrological variable for modelling the distribution of riparian plant species to guide water management decisions (Jansson et al. 2019).

The management of tropical rivers is of increasing global concern, with these understudied systems increasingly targeted for development (Dudgeon, 1992; Encalada et al., 2019; Hoeninghaus et al., 2009). In Australia, more than half of the continent's freshwater resources are in northern Australia, and development of these resources is a federal government priority (DIIS, 2015; Douglas, Bunn, & Davies, 2005; Douglas et al., 2019). For example, the Heritage-listed Fitzroy River in north-western Australia is a major tropical river with significant cultural and ecological values and yet is under increased development pressure for irrigated agriculture, potentially drawing on surface water (DIIS, 2015; Petheram, Bruce, Chilcott, Tetreault Campbell, & Watson, 2018). Water managers, development proponents and environmental practitioners are seeking information on the environmental water requirements of riverine biota, including riparian vegetation, to support sustainable water allocation planning and licensing decisions (Douglas et al., 2019). The current State government policy (DWER, 2019) precludes the construction of new dams on the river, with development instead likely to be at a smaller scale with gravity fed levees or other forms of flood capture (SMK Consultants, 2017). Proposed water policy also aims to protect key flows to maintain ecologically and culturally important assets and processes (DWER, 2020). As such, it is proposed that water-take will only occur in the wet season, and only once environmental flows of 1,500 GL of cumulative discharge in each wet season have been met (DWER, 2020). Therefore, proposed water extraction may reduce the magnitude of flood flows, reducing the extent and duration of inundation, and potentially altering the composition and extent of the riparian vegetation; however there is a paucity of ecological information to assess this risk (Douglas et al., 2019; Pollino et al., 2018). Thus, there is a pressing need to understand the relationship between flow regime attributes and the ecology of riparian plant species, as well as the outcomes of different potential water-take policies in the Fitzroy River.

The primary aim of this study was to determine how the spatial distribution of riparian woody plant species in the lower Fitzroy River floodplain might be impacted under scenarios of future water extraction. To achieve this, we developed a joint species distribution model (JSDM) which made explicit the relationship between plant occurrence and both hydrologic and non-hydrologic variables. The model was used to determine the probability of occurrence and the expected spatial distribution of species under a baseline and two water-take scenarios to assess how reduction in flow may impact the occurrence of species across the study area. This work will fulfil an immediate need to understand the ecological implications of various water take scenarios in the Fitzroy River system and increase our knowledge of the general plant ecology of the system in support of future flow management challenges. The project was undertaken using a transdisciplinary approach (Lang et al., 2012) that brought together terrestrial and freshwater ecologists, modellers, government planners and Indigenous people to address challenges of water planning and gaps in scientific knowledge (Douglas et al., 2019). The approach could be applied to other systems to assess how future scenarios, including water development and climate change, might result in changes to riverine ecosystems.

Methods

Study Area

The Fitzroy River catchment spans ~90,000 km² and is located on the south-western edge of Australia's tropical region. It experiences distinct summer wet and winter dry seasons with median monthly rainfall ranging from 0 mm (May to September) to 200 mm (January; 1991 – 2019 data collected at the Curtin Aero Gauge (-17.58, 123.83); BoM 2019). The study area has high inter-annual variability in rainfall, with a median annual rainfall of 791 mm and a range between 397 mm to 1294 mm between 1991 to 2019 (BoM 2019). Mean monthly

maximum temperatures are highest in November at 40.0 °C, with lowest maximum temperatures in June at 30.8 °C (BoM 2019). There is naturally a large variability in river discharge among years, with annual discharge at Fitzroy Crossing ranging between 468 and 19,972 GL year⁻¹, with a median of 4,232 GL year⁻¹ (years 1984-2020 at station number 802055; retrieved from bom.gov.au/waterdata/).

The study was undertaken in the lower Fitzroy River floodplain, an area extending from the town of Fitzroy Crossing in the east to Willare in the west - spanning a ~300 km stretch of the river and 3,970 km² (Fig. 1). Peak flows occur in January or February with a high degree of inter-annual variability in flood height and duration of inundation. The floodplain extends up to 15 km either side of the main river channel and contains a series of braided distributary channels which connect to the main channel in the wet season (Taylor, 1998).

Vegetation Data

To determine the distribution of woody riparian plant species we conducted vegetation surveys at 58 sites across a range of elevations and distances from the river over the dry season (July and September in 2018; Fig. 1). To ensure contrast in our data, we sampled locations that we expected to vary in flood inundation duration. Habitats sampled included those immediately adjacent to the main-channel, the top of the bank slightly further from the channel (~15-30 m from the river channel), the floodplain, banks adjacent to distributary channels, and wetlands in deflation basins on the floodplain. At each site, all woody species within a 10-m wide by 40-m long quadrat situated parallel to the main channel or floodplain distributary channel were recorded and identified to species level. Taxonomy followed Wheeler, Rye, Koch, and Wilson (1992) and Dixon (2007) and naming conventions and conservation/weed status followed those in FloraBase, the Western Australian Flora website (www.florabase.dpaw.wa.gov.au).

Permission to collect data from the sites was granted after consultation with traditional Aboriginal owners from the Walalakoo, Yi-martuwarra and Gooniyandi native title groups, and Traditional Owners and Indigenous rangers assisted with data collection. Permission was not granted by pastoralists to access sites in some areas, including around the Camballin wetlands, therefore this part of the river was not surveyed.

Hydrological variables

We used the duration of inundation (days per year) as the hydrological predictor variable of plant occurrence in our JSDM, as per Jansson, Ström, and Nilsson (2019). To capture a range of flood conditions at our sample locations, we investigated the influence of duration of inundation for two contrasting flood events. The smaller flood year (2013) represents regular flood events, which occur annually, with a 1 in 1 annual exceedance probability (AEP), overbank flows for 55 days, and maximum discharge of 69,110 ML day⁻¹ at the Fitzroy Barrage gauge (AWRC 802003; Fig. 2). The larger flood year (2000) had a 1 in 11 AEP, with overbank flows for 119 days and a substantially larger maximum daily discharge of 759,049 ML day⁻¹ at the Fitzroy Barrage gauge (Fig. 2). Inundation variables were predicted from a river discharge model (Hughes et al., 2017) and a two-dimensional hydrodynamic model (Karim et al., 2018) provided by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) through the Northern Australia Water Resource Assessment program. The output from the hydrodynamic model was a raster dataset (30-m x 30-m pixel resolution) of predicted daily water levels across the study area, which was converted to total number of days of inundation for each pixel. The number of days of inundation was extracted from the centre of each site (i.e. 10 x 40-m vegetation quadrats) for the large (2000) and small (2013) flood years as model input variables.

Environmental variables

To account for the influence of other non-hydrologic environmental factors, we included climate, soil type and fire history as covariates of species occurrence in our JSDM. Climatic variables were long-term average rainfall (R) and average monthly maximum temperature (T) which were extracted for each site from gridded spatial datasets from the Bureau of Meteorology (BoM 2018). Soil samples were collected from a maximum depth of 20 cm at each site and soil type was characterised by the percent clay content (C), determined using field texture analysis, as per (McDonald, Isbell, Speight, Walker, & Hopkins, 1998). Fire history was assessed using a remotely-sensed raster product which described the fraction of years burnt between 2005 and 2015 (Pintor, Kennard, Álvarez-Romero, & Hernandez, 2019).

Joint species distribution model

We constructed a Bayesian hierarchical JSDM to investigate how plant occurrence varied in relation to species, and hydrologic and non-hydrologic variables. Our model assumed that occurrence of plant species in our quadrats conformed to a Bernoulli distribution as, $y_{j,i} \sim \text{Bernoulli}(\psi_{j,i})$, where $\psi_{j,i}$ was the probability of occurrence of taxon j at site i . We incorporated covariates of $\psi_{j,i}$ into the model with a logit link as:

$$\text{logit}(\psi_{j,i}) = \beta_{1,j} + \beta_{2,j}I_i + \beta_{3,j}I_i^2 + \beta_4T_i + \beta_5C_i + \beta_6R_i + \beta_7F_i \quad (1)$$

where $\beta_{1,j}$ is the species-specific intercept of the model representing the average logit-scale occurrence probability of species j across sites. The parameters $\beta_{2,j}$ and $\beta_{3,j}$ represent the potential influence of flooding, i.e. duration of inundation (I), on tree occurrence. The quadratic term (I^2) was included to allow plants to show a non-linear response to inundation. The parameters $\beta_{4,j}$ through $\beta_{7,j}$ model the potential influence of the non-hydrologic variables (T = average maximum annual temperature; C = % clay in soil; R = average annual rainfall; F = fire history). Our small and large flood variables were correlated across parts of their range (i.e. the greatest number of days for each year were correlated, but diverged for

shorter duration of inundation, Figure S1.1 in the online supplement), so to account for this correlation and evaluate the relative influence of small and large floods as drivers of woody plant occurrence, we integrated both variables into a single metric of the duration of inundation as:

$$I_i = \omega I_{small,i} + (1 - \omega) I_{large,i} \quad (2)$$

where $I_{small,i}$ is the smaller flood variable and $I_{large,i}$ is the large flood variable (both centred on zero and scaled to a standard deviation of one). The parameter ω is an estimated quantity that is assumed to be uniformly distributed between 0 and 1 and serves to weight the small versus large floods in the calculation of index I_i . An estimated value of $\omega = 0.5$ indicates that both the small and large flood metrics explain the data equally well, whereas values approaching 1 or 0 indicate a stronger influence of small or large floods, respectively. All taxon-specific parameters ($\beta_{1,j} - \beta_{7,j}$) were specified as random effects drawn from Normal distributions as, $\beta_{k,j} \sim \text{Normal}(\mu_k, \sigma_k)$, where k indicates the parameter (i.e. 1-7), μ_k and σ_k are the estimated means and standard deviations of the parameter across species.

Model evaluation

We performed model evaluation with multiple approaches in a series of steps. Firstly, we evaluated general model fit of a Bernoulli error structure and a logit-normal Bernoulli error structure (to account for extra-binomial variation in the residual) using a posterior predictive distribution (Gelman, Carlin, Sterns, & Rubin, 2004) and deviance information criterion (DIC, (Spiegelhalter, Best, Carlin, & Van Der Linde, 2002)). Secondly, using the model error structure of best fit, we optimized the predictive performance of the model using a Bayesian mixture model approach referred to as Stochastic Search Variable Selection (O'Hara & Sillanpaa, 2009). This process induces model simplification through Bayesian model averaging across models with all possible combinations of covariates. We extended this

process to also model average across models that included species-specific covariate effects and shared covariate effects (i.e. equivalent effect for all species). Lastly, we determined support for each species-level covariate by inspecting the magnitude, direction, and 90 % Bayesian credible interval (CI) overlap with zero for each covariate effect parameter. We considered species-level effects statistically different from zero when the Bayesian 90 % CI did not overlap zero (approximates an $\alpha = 0.10$). Detailed modelling methods are presented in Supplementary 2.

Species occupancy under water-take scenarios

We assessed the probability of species occurrence under three scenarios: one baseline scenario which represented historical climate and current development (Hughes et al. 2017); and two water-take scenarios (300 and 600 GL). River discharge was modelled using the AWRA-R model (Hughes et al. 2018), with data provided by CSIRO and WA Department of Water and Environmental Regulation (DWER). The water-take scenarios were requested by government water planners and took into consideration proposed water allocation rules, including protection of “first-flush” flows and minimum levels to protect aquatic biota (Douglas et al., 2019). For the water-take scenarios 300 gegalitres (GL) and 600 GL of water were extracted from the system, spread across eight water-take points. To comply with proposed water planning policy water-take only occurred in the wet season, once cumulative flow for each wet season was greater than 1,500 GL (DWER, 2020; Table S.1.1). The water-take scenarios resulted in a small change in flow in the large flood year (2011), with a less than 2% change in total discharge under both the 300 GL and 600 GL scenarios (Fig. 2a). For the smaller, regular flood (1 in 1 AEP; 2013), the 300 GL water take resulted in a 7 % decrease in total annual discharge and the 600 GL a 15 % decrease (Figure2b).

River discharge data were inputted into a two-dimensional hydrodynamic model (Karim et al. 2018), producing raster datasets of duration of inundation for each scenario (baseline, 300 GL and 600 GL water-take). The inundation values were applied to the JSDM, producing raster datasets of probability of species occupancy. Total species occupancy across the study area was then determined by summing all pixels and calculating the total area of habitat for each species for each scenario. Manipulation and analysis of raster datasets was completed in R (R Core Team 2017), maps were produced in ArcGIS (v. 10.5.1), and models were run in program JAGS (Plummer, 2003) called by program R using the R2jags package (Yu-Sung & Yajima, 2015).

Results

A total of 26 woody species were recorded, and the most abundant species (> 200 individuals) were *Barringtonia acutangula*, *Atalaya hemiglauca*, *Eucalyptus microtheca*, and *Eucalyptus camaldulensis* (Table S1.2). Only three woody weed species were observed, and only in low numbers (Table S1.2). However, in some higher elevation sites and the top of riverbanks there was a significant (up to 70 %) cover of herbaceous weed species, particularly *Jatropha gossypifolia* and *Xanthium strumarium*. Eight woody species had a total abundance of less than five individuals across all study sites (Table S.1.2). Our model fit procedure indicated that the Bernoulli error structure was the best approximating model from which we drew all further inference. Detailed model fit and reduction results are presented in Supplementary 2.3.

Our model indicated that the duration of inundation was the strongest driver of riparian woody plant species occurrence in our study region, predicting species occurrence better than rainfall, temperature, long-term fire history, or clay content of the soil (Table 1). This was evidenced by the effect sizes for environmental parameters, with larger effect sizes for the

inundation metric (Figure 3b,c) than for the non-hydrological variables (Figure 3d-g). For example, the main and quadratic effects of inundation ranged from -0.76 to 1.80, with six species having statistically significant main effects and all species having statistically significant quadratic effects (Figure 3b,c). In contrast, the effect sizes of the non-hydrological variables never exceeded 0.02 (Figure 3d,e,f,g). The relative importance of hydrological drivers was further supported by the greater variety of responses among species to the inundation metric, with positive and negative effect sizes for this variable (Figure 3b), while responses to the non-hydrological variables were unidirectional for all species (Figure 3d-g). Lastly, our model suggested that smaller, more frequent floods (2013, 1 in 1 AEP) were more influential for determining riparian tree occurrence than larger, less frequent floods (2000, 1 in 11 AEP). This was evidenced by the estimated weighting parameter $\omega = 0.77$; however, this parameter estimate was highly uncertain (i.e. 90 % CI = 0.35, 0.98).

Species distribution

The spatial distribution and maximum probability of occurrence varied among species. Maximum probability of occurrence was greatest for *B. acutangula*, at 0.79, compared with 12 rarer species that had a maximum probability of occurrence of less than 0.07 (Table 2). The distribution of species under the baseline scenario varied among species. *Eucalyptus microtheca* had the greatest distribution, covering 2,795 km² within the study area (which had a total area of 3,971 km²) (see Table 2 bottom row). The highest probability of occurrence for *E. microtheca* was across extensive areas of floodplain which receive relatively shorter inundation durations, which was reflected in the effect size, with a significant negative response to the inundation metric (Fig. 3b). *Eucalyptus camaldulensis* also covered a relatively large area, i.e. 1,424 km², although the species was associated with wetter environments than *E. microtheca*, as evidenced by a more positive effect size for the inundation metric (Fig. 3b). *Atalaya hemiglauca* was found to often co-occur with *E.*

camaldulensis, with a similar effect size and covering a similar area under the baseline scenario (Table 2; Fig. 3b).

Species associated with wetter environments, as indicated by positive effect sizes for the inundation metric, were *Melaleuca argentea*, *Melaleuca leucadendra*, *Nauclea orientalis*, *Barringtonia acutangula* and *Bridelia tomentosa* (Fig. 3b). These species were restricted to wetter environments, particularly along the main channel of the river and large distributary channels in the floodplain (e.g. see map of occupancy for *M. argentea* in Fig. 4a).

Barringtonia acutangula had the greatest distribution out of the species associated with wetter conditions, covering an area of 925 km² under the baseline scenario, compared with 128 km² for *N. orientalis* and 388 km² for *M. leucadendra* (Table 2)

Water-take scenarios

Across the study area, there was little change to the duration of inundation (shown as the inundation metric) under the two water-take scenarios (Fig. 5). There were only small changes in *I* for areas with the highest number of days of inundation (*I* between 0.6 and 1.03, or the 91st and 100th percentiles), particularly along the main river channel. The greatest reduction occurred away from the main river channel along large distributary channels, particularly in downstream sections of the lower Fitzroy river (Fig. 5), where *I* was between -0.40 and 0.10 (89th and 90th percentiles of *I*). Large areas of floodplain with the shortest duration of inundation (with *I* between the 1st and the 25th percentile showed no change under the two water-take scenarios (Fig. 4). The 600 GL water-take scenario showed the greatest change in the pattern of inundation compared to baseline (Fig. 5).

Under the two water-take scenarios there were small reductions in the distribution of species associated with wetter environments. For example, the distribution area of *M. argentea* declined by 7.4 % under the 600 GL water-take scenario compared to the baseline (Table 2). Similar reductions were found for *M. leucadendra* (-6.2 %) and *N. orientalis* (-7.0 %) (Table

2), and the reduction of these species was most pronounced in downstream areas (eg. *M. argentea* in Fig. 4). More than a third (10 out of 26) of species decreased by between 3 and 5 % in the 600 GL water-take scenario compared with the baseline. Changes were smaller under the 300 GL water-take scenario, with *M. argentea* showing the greatest decrease of 1.5 %. Species associated with drier environments (as indicated by more negative effect sizes for the inundation variable) had a negligible (less than 1 %) change under both water-take scenarios, and the species associated with the shortest duration of inundation, *E. microtheca*, was found to have a very small increase in area, increasing by 5.4 km², or 0.2 % under the 600 GL water-take scenario (Table 2 bottom row).

Discussion

Our JSDM linked the occurrence of riparian trees to hydrological models used by state government regulators, providing outputs to directly inform water planning decisions. We found that the hydrological variable was the strongest predictor of species occurrence, and that the model is effective for predicting change in the probability of species occurrence under water-take scenarios. Our approach resulted in maps of predicted habitat availability for 26 woody species on the floodplain of the Fitzroy River, critical information to assist decision making in this severely data deficient system. Most species had small distributions and were associated with wetter parts of the landscape along the main river channel and large distributary channels. Species associated with drier environments, including *E. microtheca* and *B. cunninghamii* were more widely distributed, covering a significant part of the study area that does not receive a long duration of inundation. Under the water-take scenarios, many species, particularly those with preferences for drier environments, showed a negligible change in occupancy area; however, species constrained to the wettest environments did decline. Species declines were confined to the downstream sections of the Fitzroy,

highlighting how the impact of water-take can occur at a localised scale rather than consistently across a landscape.

Under the assessed water-take scenarios the species with the greatest decline in predicted occupancy were those with a preference for wetter environments. In particular, *M. argentea*, *M. leucadendra*, *N. orientalis* and *B. acutangula* decreased under the 600 GL water-take scenario compared with the baseline. These species are likely to have high water requirements, with *B. acutangula* and *M. leucadendra* shown to use groundwater or deep stored soil moisture in the dry season (Lamontagne et al., 2005; O'Grady, Eamus, Cook, & Lamontagne, 2006). A reduction in wet-season flood flows may reduce recharge of the water stores required for the persistence of these species in the dry season. Species that fringe rivers and large creeks, such as *M. argentea*, have physiological traits that confer a high tolerance of flood conditions, experiencing submergence in fast flowing water during the wet season (Alexander, Fielding, & Jenkins, 1999; Fielding & Alexander, 2001; McLean, 2014). For example, the two *Melaleuca* species have flexible stems and hard leaves, and the seedlings of *E. camaldulensis* develop extensive adventitious roots (Argus et al., 2015) that help plants survive significant flooding. These species may be selected for in wetter environments, however, if conditions become drier, our model indicates wetter species could experience a decline in area, and potentially be replaced by more xeric species, such as *E. microtheca*.

The proposed management of the Fitzroy River aims to protect key flows to maintain ecological assets and processes, to support habitat for terrestrial fauna and to maintain riparian vegetation in its own right (DWER 2020). We found that this goal would be met under the 300 GL water-take scenario, with all woody plant species showing a decline of <1.5 %. However, under the 600 GL water-take scenario our study suggests that the total occupancy area of 14 species associated with wetter conditions will decline between 2 and 7.5 % across the study area. The relatively small reductions in species occupancy may merely

reflect the relatively small amount of water-take investigated in our scenarios; however, it may also be due to many of the species being adapted to limited or variable water supply. Indeed, many of the woody species present in the study area have wide geographic distributions, including areas of Australia with low and/or intermittent rainfall.

Our spatially-explicit predictions also revealed that species declines were most pronounced in particular locations. For example, under the 600 GL water-take scenario the area of *M. argentea* was predicted to decline by 19 km², with most of this decline occurring along the large distributary channels downstream of Camballin. We were unable to sample large parts of this reach; however, we are confident that our model predictions apply to this area because we assessed rainfall, temperature and evaporation along the length of the river and found no difference in climate. The area around Camballin also has similar soils to the areas we sampled (See <https://nawra-explorer.csiro.au/#soil>). Given this location is predicted to show the greatest impact to water-take we strongly recommend research and monitoring be undertaken here, particularly along the distributary channels that are predicted to be most impacted. These channels support riparian plant species including *M. argentea* and *B. acutangula*, which do not otherwise occur on the floodplain, and reductions in flow and decline of riparian species may have important ecological implications.

A reduction in riparian plant species, both along the main river channel and along distributary channels can alter the structure and function of the riverine system (White & Stromberg, 2011). *Melaleuca* species form thick root mats (McLean, Ludwig, & Grierson, 2011), and play an important role in bank stability. A reduction of these riverbank species could result in erosion along the river and distributary channels, altering river geomorphology (Perucca, Camporeale, & Ridolfi, 2007). A reduction in riparian trees may also impact instream biota. The leaves of tree species fringing the river, including *M. argentea*, *M. leucadendra* and *B. acutangula*, are a source of energy in the aquatic food web (Beesley et al., 2020; Hladyz,

Nielsen, Suter, & Krull, 2012), and old fallen trees provide habitat for fish (Crook & Robertson, 1999). Large tropical river trees are also important habitat for terrestrial biota such as reptiles and amphibians (Semlitsch & Bodie, 2003), birds (Skroblin & Legge, 2012) and bats (Bennett et al., 2014). Not enough is known about the ecology to predict if small changes (< 1.5% for 40 % of species) in vegetation will impact the ecological function. However, localised reductions of species such as *M. argentea*, *M. leucadendra*, *N. orientalis* and *B. acutangula* along distributary channels, could have significant effects on the ecological functioning of the river system in that location.

Cultural values may also be impacted if riparian vegetation is impacted by water-take. Many riparian tree species, including those predicted to decline under water-take scenarios, have significant cultural values for the Indigenous people of the lower Fitzroy River. Some species have cultural use values, providing food, or being used in the preparation of food. For example the bark of *M. leucadendra* (*kurrumpa* in Walmajarri; Nuggett, Nuggett, Bangu, & Woodward) is commonly used to wrap fish, such as Barramundi, for cooking in a campfire. *Bridelia tomentosa* (*ngoojiny* in Nyikina) has black berries that are collected and eaten during the flood time (*warramba* in Nyikina; (Milgin, Nardea, Grey, Laborde, & Jackson, 2020)). *Barringtonia acutangula* (*gooroo* in Gooniyandi), has multiple uses. Its leaves may be crushed and used as an anaesthetic, and are also used to stun fish to facilitate capture to allow hunting (Davis, Street, Malo, Chereil, & Woodward, 2011), and the species is central to creation stories, with deep cultural significance (Milgin, Nardea, Grey, Laborde, & Jackson, 2019). Changes to the distribution of vulnerable plant species through water development has the potential to impact on cultural values. Equitable water management should take into consideration the potential impact that water-take will have on culturally significant species and seek input from Indigenous communities throughout the planning process (Douglas et al. 2019).

To achieve our aim of providing information to managers in a data-limited environment we used data from the hydrodynamic model being used to inform management decisions. As other hydrodynamic models become available for the study area there is an opportunity to refine our JDSM to assess other scenarios including projected climate scenarios. Future research could model the interaction between water-take and a changing climate and the impact on riparian trees. In addition to surface water flows, groundwater levels are likely to influence the distribution of species (O'Grady et al., 2006; Pettit & Froend, 2018).

Unfortunately, the depth to groundwater was not known for the study sites and it was not feasible to collect these data. We encourage future research to assess the groundwater dependency of riparian vegetation on the Fitzroy River.

Other factors that may influence species distribution that were not taken into consideration in our study include the distribution of seed and germination requirements for different species. It is likely particular hydrological conditions are required for the successful recruitment of these riparian species (Pettit & Froend, 2001), and identifying these requirements will improve our ability to predict the persistence of species under different water scenarios. Fire may also influence the composition of riparian trees (Douglas et al. 2015). Our model showed that fire had a negligible effect on species occurrence, however fire impacts were not the focus of the current study, and a more targeted approach using finer scale metrics would be required to further assess the impact of fire on riparian plants on the Fitzroy River.

Many species had a low maximum probability of occurrence of less than 0.07 for 12 species, which may indicate several things: a species may be naturally rare; the size of our sample plots was too small to sufficiently detect species; or, species occurrence is influenced by factors not included in our model. The vegetation in the lower Fitzroy is generally sparse and patchy, therefore, across the study area there are many species that have a naturally rare

occurrence. To increase the detection of rarer species, future studies would benefit by increasing the size and number of sample plots.

We undertook this project using a transdisciplinary approach (Lang et al 2012, Douglas et al 2019) to provide timely and applicable information to government water regulators about how riparian vegetation on the Fitzroy River might change under different policies. The team included staff from the authority tasked with decision-making about water allocation and licensing in a region with little hydrological and ecological data available. Collaboration with the end-users of the research (including R. Loomes who is an author) ensured we used the same hydrological data and scenarios that government hydrologists and ecologists use in their assessment of environmental water requirements for the Fitzroy River. The scenarios assessed were informed by the water-take policies being considered as part of a water allocation plan; however, the model may also be readily applied to other scenarios, for example in response to specific water license applications. Maps of predicted species occurrence generated by this study are directly useful for managers, particularly in this data-poor environment with limited vegetation mapping and no data linking flow to vegetation. In particular, maps that highlight areas most susceptible to changes in flow will assist management to protect ecological and cultural values.

Conclusions

Globally there is a high demand for data directly relating flow to community dynamics, in order to understand how future scenarios (such as water development, climate change or both) might result in changes to riverine ecosystems (Stoffels, Bond, & Nicol, 2018). Our approach identified flood inundation as a driver of the distribution of riparian tree species across the floodplain, allowing us to predict change in species distribution under different water-take scenarios. We found that the proposed management goal to have minimal change

in the distribution of riparian plant species would be met under the 300 GL water-take scenario, with < 1.5 % decline for all species. However, under the 600 GL water-take scenario eight species declined by more than 5 %. We found that species associated with wetter environments, including *M. argentea*, *M. leucadendra*, *N. orientalis* and *B. acutangula* had the greatest decline in occupancy area under water-take scenarios. Our results highlight that water managers should consider the impact of water-take on species associated with wetter environments. Furthermore, mapping outputs highlighted areas most likely to be impacted by water-take, which in this system included the large distributary channels downstream of Camballin. Future water planning is encouraged to consider how changes in flood extent and duration of inundation may impact ecologically and culturally significant plant species both across the floodplain and in localised areas identified as vulnerable to change.

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Data availability statement

Data is available through the University of Western Australia's research repository (<https://research-repository.uwa.edu.au/en/datasets/>).

Conflict of interest statement

No conflict of interest has been declared by the author(s).

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Tables

Table 1. Model selection results. The posterior probability that the parameter in the far-left column is equal to zero (2nd column), non-zero but invariant among species (3rd column), or a species-specific random effect (4th column). The parameters are: inundation metric ($\beta_2 (I_i)$); inundation metric squared ($\beta_3 (I_i^2)$); mean daily maximum temperature ($\beta_4(T_i)$); % clay content of soil ($\beta_5 (C_i)$); mean annual rainfall ($\beta_6 (R_i)$); and, fire history as a fraction of years burnt ($\beta_7 (F_i)$).

Parameter	<u>Zero</u> $\beta_{k,j} = 0$	<u>Invariant</u> $\beta_{k,j} = \mu_k$	<u>Species-specific</u> $\beta_{k,j} = N(\mu_k, \sigma_k)$	<u>Total</u> <u>inclusion</u> <u>in model</u>
$\beta_2 (I_i)$	0.00	0.00	1.00	1.00
$\beta_3 (I_i^2)$	0.24	0.41	0.35	0.76
$\beta_4 (T_i)$	0.44	0.14	0.42	0.56
$\beta_5 (C_i)$	0.62	0.16	0.22	0.38
$\beta_6 (R_i)$	0.89	0.07	0.04	0.11
$\beta_7 (F_i)$	0.70	0.18	0.12	0.30

Table 2. Summary table showing the maximum probability of a species occurrence (Max. Prob.) in relation the number of days of inundation as predicted from a joint species-distribution model, total occupancy area (km²) for each species under a baseline (BL), 300 GL and 600 GL water-take scenarios, and percent (%) change in area occupied between the water-take scenario (300 GL and 600 GL water-take).

	Max. Prob	Total area (km ²)			% change 300GL	% change 600GL
		BL	300GL	600GL		
<i>Melaleuca argentea</i>	0.41	249	245	230	-1.5	-7.4
<i>Melaleuca leucadendra</i>	0.39	388	384	364	-1.2	-6.2
<i>Nauclea orientalis</i>	0.16	128	126	119	-1.4	-7.0
<i>Barringtonia acutangula</i>	0.79	925	915	875	-1.0	-5.4
<i>Bridelia tomentosa</i>	0.31	394	390	373	-1.0	-5.2
<i>Santalum lanceolatum</i>	0.04	53	52	50	-1.0	-4.9
<i>Melaleuca nervosa</i>	0.04	54	53	51	-0.9	-5.0
<i>Planchonia careya</i>	0.04	54	54	52	-1.0	-5.0
<i>Parkinsonia spp.*</i>	0.04	54	54	52	-0.9	-5.0
<i>Lophostemon grandiflorus</i>	0.04	55	54	52	-0.9	-4.9
<i>Ficus coronulata</i>	0.27	459	456	443	-0.7	-3.7
<i>Acacia colei</i>	0.19	338	336	326	-0.6	-3.4
<i>Terminalia platyphylla</i>	0.36	783	779	765	-0.4	-2.3
<i>Azadirachata indica*</i>	0.04	66	66	64	-0.6	-3.5
<i>Eucalyptus camaldulensis</i>	0.57	1,424	1,421	1,403	-0.2	-1.5
<i>Atalaya hemiglauca</i>	0.51	1,321	1,317	1,302	-0.3	-1.4
<i>Calotropis procera*</i>	0.11	246	245	241	-0.4	-1.9
<i>Carissa lanceolata</i>	0.04	88	88	87	-0.3	-1.4
<i>Ficus racemosa</i>	0.04	89	88	87	-0.3	-1.4
<i>Corymbia bella</i>	0.35	984	982	975	-0.2	-0.9
<i>Vachellia farnesiana*</i>	0.06	158	158	157	-0.1	-0.7
<i>Ficus aculeata</i>	0.06	166	166	165	-0.1	-0.4
<i>Melia azedarach</i>	0.06	164	164	163	-0.1	-0.4
<i>Corymbia greeniana</i>	0.06	174	174	174	0.0	0.1
<i>Bauhinia cunninghamii</i>	0.26	821	821	822	0.0	0.1
<i>Eucalyptus microtheca</i>	0.76	2,795	2,797	2,801	0.0	0.2

Figure legends

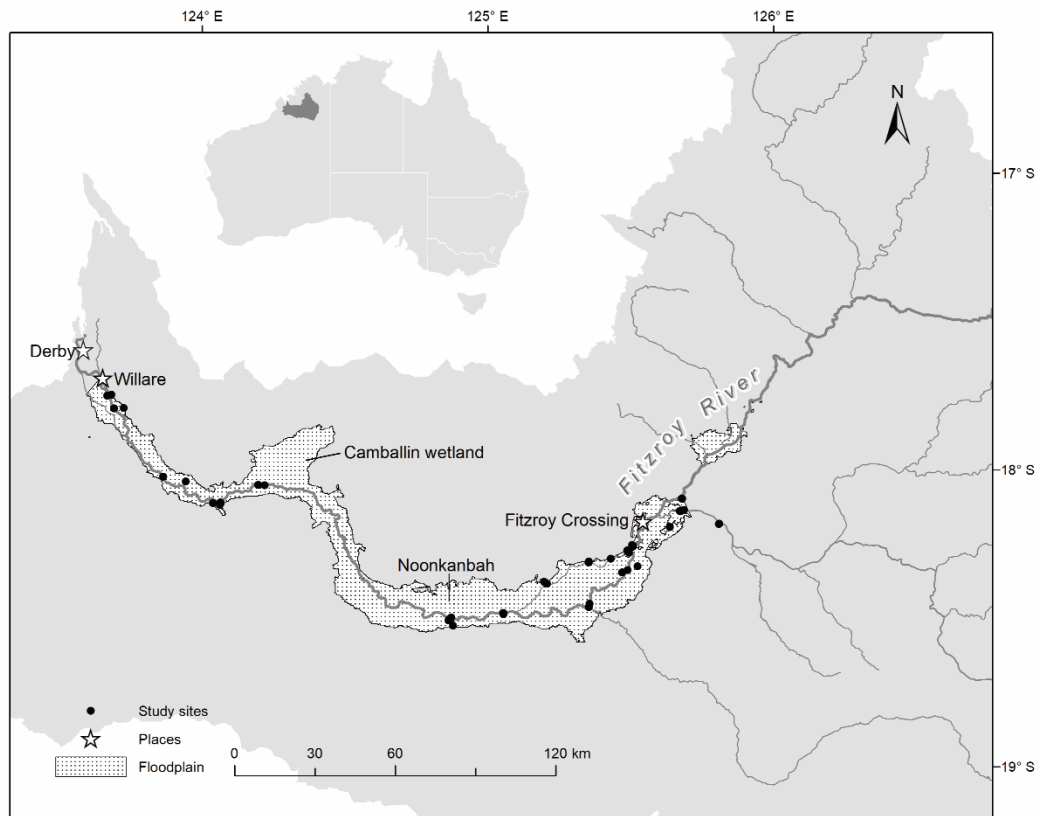


Figure 1. Map of study area showing the location of survey sites (circles) and locations referred to in the main text, including the towns of Fitzroy Crossing and Derby (stars).

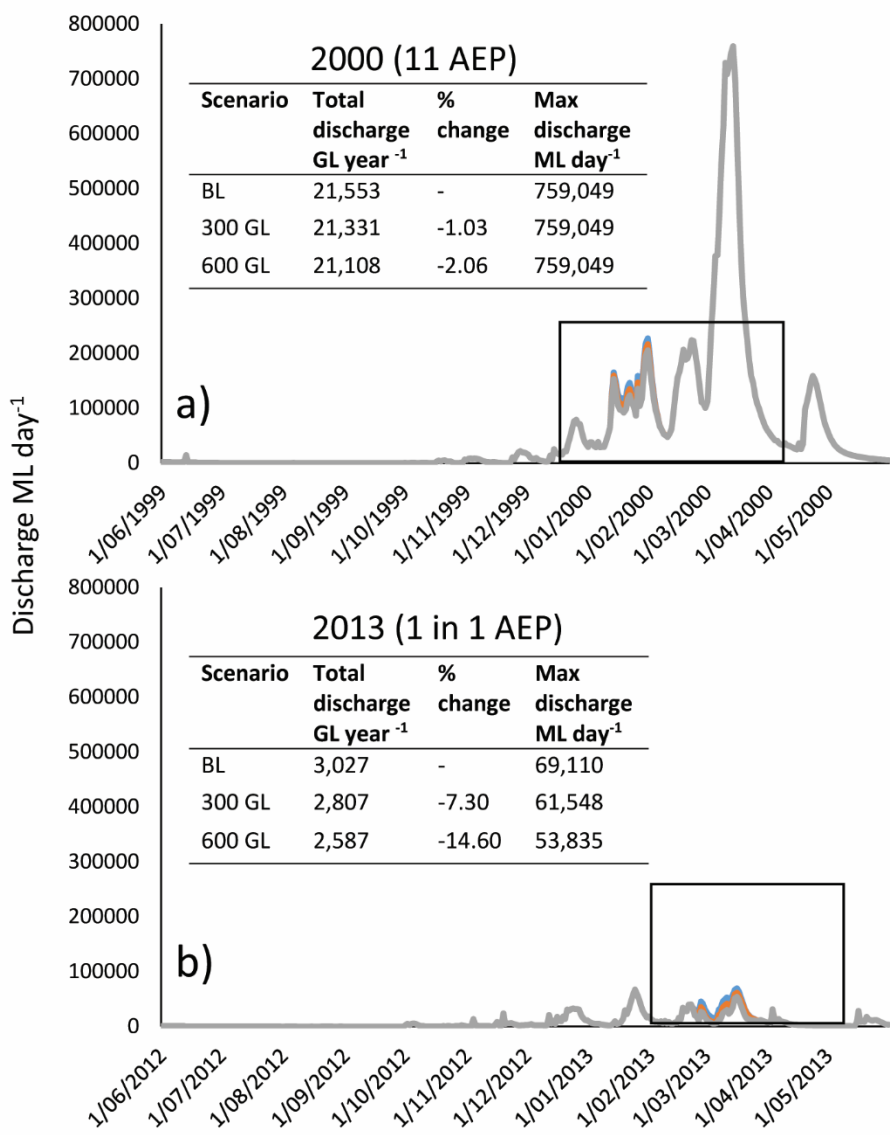


Figure 2. Modelled daily river discharge (using the AWRA-R model; Hughes et al. 2018) at Fitzroy Barrage in a 1 in 11 annual exceedance probability (AEP) flood (year 2000; a) and a 1 in 1 AEP flood (2013; b) under baseline (blue line), 300 GL (orange) and 600 GL (grey) water-take scenarios. Black rectangle shows the period modelled for flood inundation. Data in table insets show the total annual and maximum discharge for each year under the three scenarios, as well as the percent change in total annual discharge from the baseline scenario.

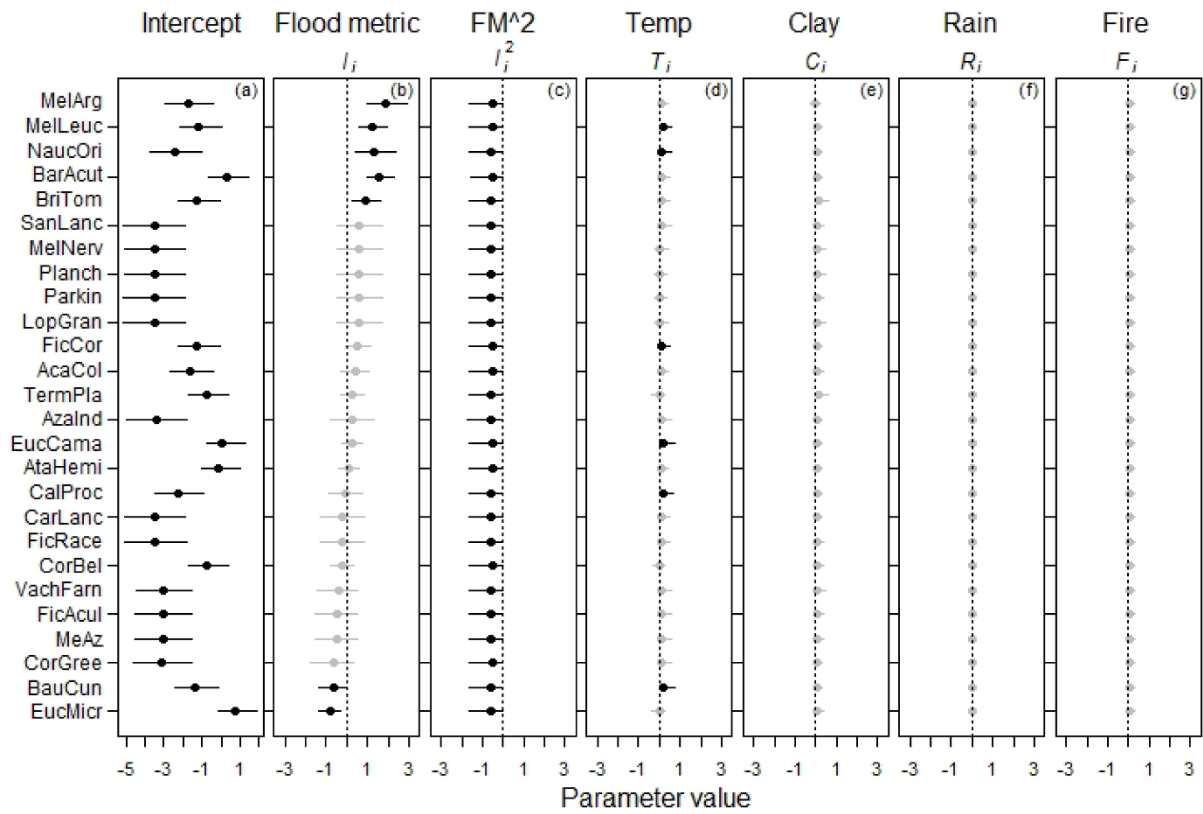


Figure 3. Summary of effect size for the following covariates: flood metric (equation 1), square of the flood metric (FM^2), average monthly maximum temperature (Temp), percent clay in soil (Clay), average annual rainfall (Rain), and fire frequency (Fire). Refer to Table S1.2 for full species names. The dots represent the posterior means while the error bars indicate the 90% Bayesian credible intervals. The colour black indicates when the point estimate is statistically different to zero at $\alpha = 0.10$.

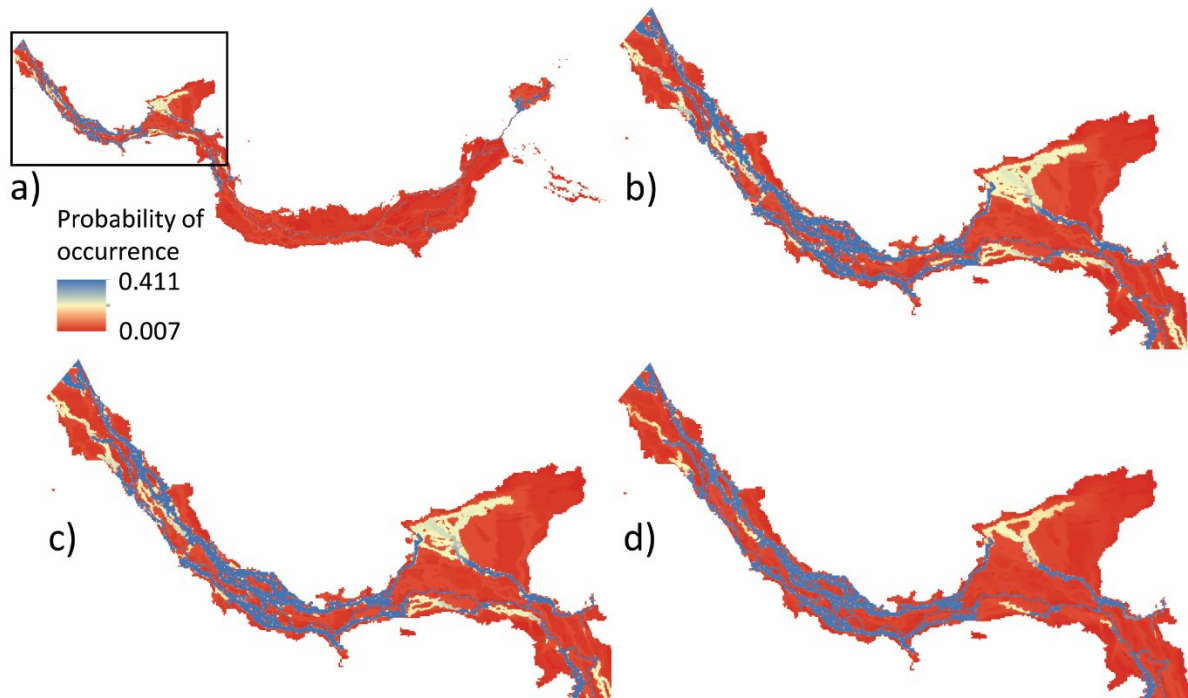


Figure 4. The probability of occurrence for *Melaleuca argentea* under different scenarios. Panel (a) shows the whole study area under the baseline scenario. The area most impacted by water-take is highlighted showing predicted *M. argentea* occurrence under the baseline (b), 300 GL (c) and 600 GL (d) water-take scenarios. Area shown is most impacted by water-take, with the whole study area shown as inset.

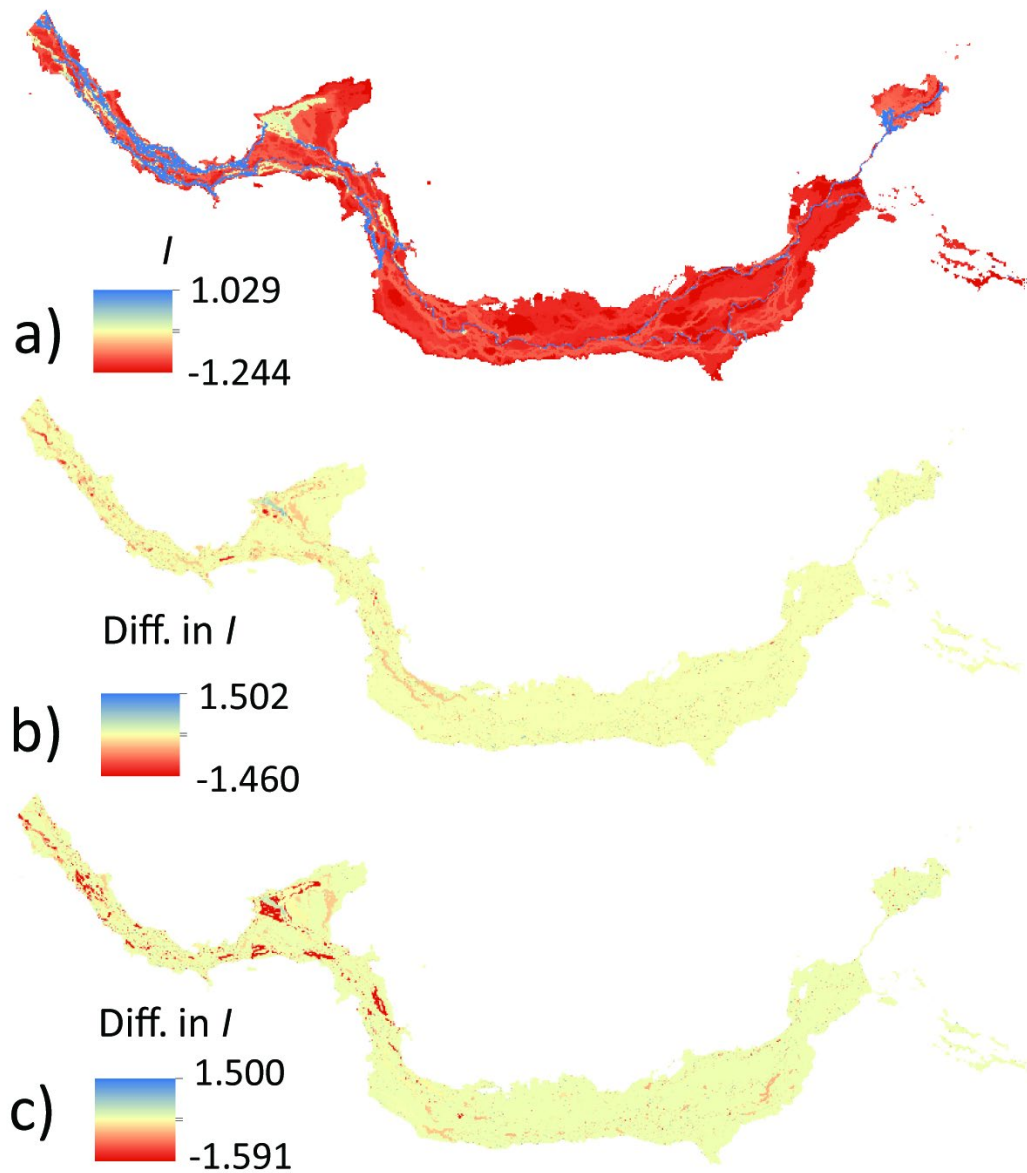


Figure 5. Maps showing (a) values for the inundation metric (I) which is a summary variable derived from the number of days of inundation in a small and a large flood, and the difference in I between the baseline and a 300 GL (b) and 600 GL (c) water-take scenarios.

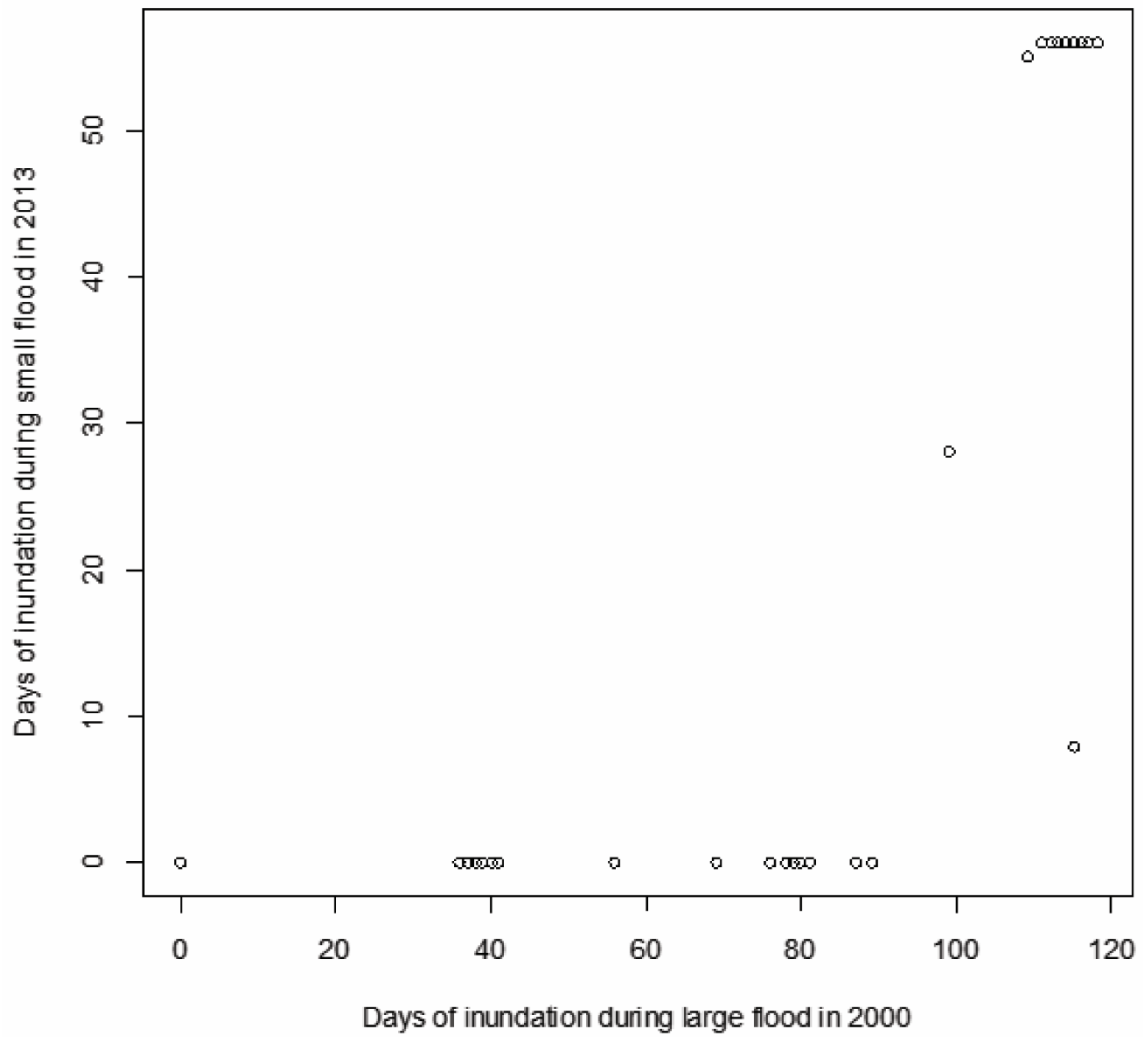


Figure S.1.1 Relationship between the number of days of inundation in the large flood year (2000) and the small flood year (2013). Data shown is the number of days of inundation for each of the 58 study sites, extracted from outputs of the 2-dimensional hydrodynamic model (Karim et al. 2018).

Supplementary 1: Supporting information cited in the main-text

Table S.1.1. Inputs into the river model simulation (AWRA-R; Hughes et al. 2018; CSIRO 2020) for the 300 GL and 600 GL water-take scenarios. Water-take was spread across 8 nodes, with the maximum pumped volume from all nodes equalling a total of 300 GL and 600 GL annual water-take.

Node ID	Maximum pumped volume (GL/year)		Maximum pump rate (ML/day)		Pump start threshold (ML/day)		Requirement of the system (GL/year)	
	300 GL	600 GL	300 GL	600 GL	300 GL	600 GL	300 GL	600 GL
8020552	25	50	1250	2500	500	500		
8020062	2.5	5	125	250	0	0		
8022030	25	50	1250	2500	500	500		
8020554	25	50	1250	2500	1600	1600		
8020550	57.5	115	2875	5750	2600	2600		
8020060	30	60	1500	3000	2600	2600		
8020030	65	130	3250	6500	3000	3000	1500	1500
8020070	70	140	3500	7000	3000	3000		

Table S.1.2. Woody species identified in vegetation surveys at 58 study sites along the Fitzroy River and its floodplain. The count shows the total number of individuals recorded across all sites.

Code	Family	Species	Habit	Count
CalProc	Apocynaceae	* <i>Calotropis procera</i> (Aiton) W.T.Aiton	Shrub or tree	19
CarLanc	Apocynaceae	<i>Carissa lanceolata</i> (R.Br.)	Shrub	3
TermPla	Combretaceae	<i>Terminalia platyphylla</i>	Tree	60
AcaCol	Fabaceae	<i>Acacia colei</i> Maslin & L. Thomson	Shrub or tree	14
BauCun	Fabaceae	<i>Bauhinia cunninghamii</i> (Benth.) Benth.	Tree or shrub	18
Parkin	Fabaceae	<i>Parkinsonia aculeata</i> L.	Shrub or tree	2
VachFarn	Fabaceae	* <i>Vachellia farnesiana</i> (L.) Wight & Arn.	Tree or shrub	2
BarAcut	Lecythidaceae	<i>Barringtonia acutangula</i>	Tree or shrub	363
Planch	Lecythidaceae	<i>Planchonia careya</i> (F. Muell.) R. Knuth	Tree or shrub	1
Azalnd	Meliaceae	* <i>Azadirachta indica</i> A. Juss.	Tree	1
MeAz	Meliaceae	<i>Melia azerdarach</i> L.	Tree	4
FicAcul	Moraceae	<i>Ficus aculeata</i> Miq.	Shrub or tree	27
FicCor	Moraceae	<i>Ficus coronulata</i> Miq.	Tree	51
FicRace	Moraceae	<i>Ficus racemosa</i> L.	Tree	3
CorGree	Myrtaceae	<i>Corymbia greeniana</i> (D.J.Carr & S.G.M.Carr) K.D.Hill & L.A.S.Johnson	Tree	8
CorBel	Myrtaceae	<i>Corymbia bella</i> (K.D.Hill & L.A.S.Johnson)	Tree	86
EucCama	Myrtaceae	<i>Eucalyptus camaldulensis</i> Denh.	Tree	212
EucMicr	Myrtaceae	<i>Eucalyptus microtheca</i> F. Muell.	Tree	310
LopGran	Myrtaceae	<i>Lophostemon grandiflorus</i> (Benth.) Peter G.Wilson & J.T.Waterh.	Tree	11
MelArg	Myrtaceae	<i>Melaleuca argentea</i> (W.Fitz)	Tree	131
MelLeuc	Myrtaceae	<i>Melaleuca leucadendra</i> (L.) L.	Tree	132
MelNerv	Myrtaceae	<i>Melaleuca nervosa</i> (Lindl.) Cheel	Tree or shrub	11
BriTom	Phyllanthaceae	<i>Bridelia tomentosa</i> Blume	Tree or shrub	116
NaucOri	Rubiaceae	<i>Nauclea orientalis</i> (L.) L.	Tree	14
SanLanc	Santalaceae	<i>Santalum lanceolatum</i> R. Br.	Shrub	5
AtaHemi	Sapindaceae	<i>Atalaya hemiglauc</i> a (F. Muell.) Benth.	Tree or shrub	249
Total				1853

* Indicates non-native species

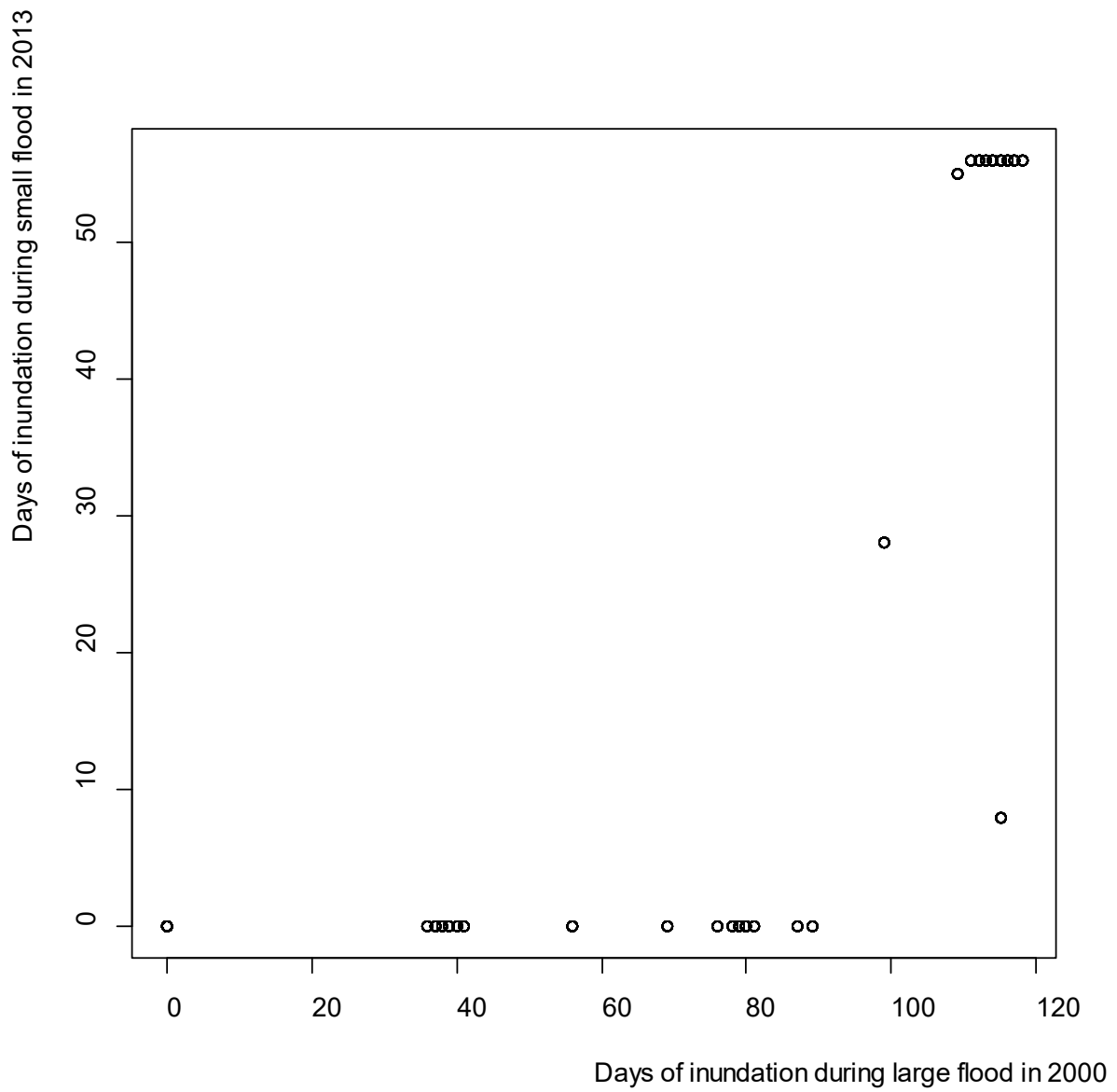


Figure S.1.1 Relationship between the number of days of inundation in the large flood year (2000) and the small flood year (2013). Data shown is the number of days of inundation for each of the 58 study sites, extracted from outputs of the 2-dimensional hydrodynamic model (Karim et al. 2018).

Supplementary 2. Joint-species distribution modelling methods

Supplementary 2.1. Model evaluation

We considered all possible combinations of species-level covariates, where covariate effects can be zero and equivalent among species, non-zero and equivalent among species, or non-zero and variable among species. Additionally, we considered two possible model error structures as plausible models, which resulted in a daunting 1,458 plausible models. The high dimensionality of this model selection problem, prevented the exclusive use of iterative and computationally expensive model selection procedures such as multi-model inference with information theoretic criterion (e.g. Akaike Information Criterion (AIC), Burnham and Anderson (2002), Deviance Information Criterion (DIC), Spiegelhalter et al. (2002)) and k-fold cross validation (Broms et al. 2016). Thus, we performed our model evaluation with multiple approaches in a series of steps. Firstly, we evaluated general model fit of two possible model error structures using a posterior predictive distribution (Gelman et al. 2004) and deviance information criterion (DIC, Spiegelhalter et al. 2002). Secondly, using our best model error structure, we evaluated support for each covariate at the community level with a Bayesian mixture model approach (O'Hara and Sillanpaa 2009). Lastly, we determined support for each species-level covariate by inspecting the magnitude, direction, and 90 % Bayesian credible interval (CI) overlap with zero for each covariate effect parameter. We considered species-level effects statistically different than zero when the Bayesian 90 % CI did not overlap zero (approximates an $\alpha = 0.10$).

We considered two general model error structures and evaluated model fit for each, including all covariates with variable effects across species, using the posterior predictive distribution (Hooten and Hobbs 2015, Broms et al. 2016). The first error structure assumed that the incidence data resulted from a simple binomial sampling process, while the second allowed for additional extra-binomial variation in the incidence data. We specified the second error structure by including a sample-level random effect that was normally distributed on the logit scale (i.e. $\text{logit}(\psi_{j,i}) = \Psi_{j,i} + \varepsilon_{j,i}$). We evaluated the fit of each of the error structures by simulating each data point from the posterior distributions of the model parameters and calculating the cumulative probability of correctly classifying both zero and non-zero data points. Additionally, we calculated the deviance information criterion for each model to determine the level of parsimony. We considered the model with the lowest DIC with adequate model fit as the best error structure and applied it for further analysis and inference.

We evaluated support for each covariate using a Bayesian mixture-model approach termed Stochastic Search Variable Selection (SSVS). Using SSVS to produce models with desirable predictive properties was first introduced by George and McCulloch (1993) but has been thoroughly discussed in more

recent ecological literature (O'Hara and Sillanpaa 2009, Tenan et al. 2014, and Hooten and Hobbs 2015). Here we use a modified form of SSVS to evaluate support for each β parameter as species-specific (i.e. $\beta_{k,j} \sim \text{Normal}(\mu_k, \sigma_k^2)$, invariant across species (i.e. $\beta_{k,j} = \mu_k \sim \text{Normal}(0,100)$) or equal to zero (i.e. excluded from the model, $\beta_{k,j} = \mu_k = 0$). We achieved this by including a set of indicator variables into our model. Typically, these indicators are binary draws from a Bernoulli distribution and indicate when a parameter is included or excluded from the model. For our model selection problem, we include and exclude sets of parameters, thus the prior for each indicator variable was specified as $I_k \sim \text{Categorical}\left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right)$, indicating equal prior support for either of the three hypotheses for each covariate. The posterior values of the indicator variables can be interpreted as support for the predictive potential of the model term, similar to the posterior probabilities for different model structures obtained via reversible jump methods (Green 1995). However, one advantage of the SSVS process is that model predictions are automatically model averaged, providing a more refined level of regularization and accounting for structural uncertainty.

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Supplementary 2.2. Model fitting methods and code for multi-taxa model.

The posterior distributions of all parameters were estimated using a Gibbs sampler implemented in JAGS (Plummer 2003). We called JAGS from program R (R Core Team 2015) using the library R2jags (Su and Yajima 2015). All prior distributions of logit-scale effect parameters (μ_1 - μ_5) were specified as diffuse normal distributions. Priors for precision parameters (σ_1 - σ_5) were specified as uniform distributions with a range between 0.01 and 100 and were verified to not influence the range of posterior distributions. Inference was drawn from 10,000 posterior samples taken from two chains of 10^6 samples thinned to every 100. We discarded the first 500,000 values of each chain to remove the effects of initial values. Convergence was diagnosed for each model by visual inspection of the MCMC chains for adequate mixing and stationarity and by using the Gelman-Rubin statistic (with values < 1.1 indicating convergence; Kery 2010, Gelman et al., 2004).

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Gelman A., J.B. Carlin, H.S. Stern, and D.B. Rubin. 2004. Bayesian Data Analysis. Boca Raton: Chapman and Hall.

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Parameter definitions:

$\text{bet}[1,\text{spec}[i]] = \beta_{1,j}$ = taxa-specific intercept.

$\text{bet}[2,\text{spec}[i]] = \beta_{2,j}$ = taxa-specific effect of inundation metric.

$\text{bet}[3,\text{spec}[i]] = \beta_{3,j}$ = taxa-specific quadratic effect of inundation metric.

$\text{bet}[4,\text{spec}[i]] = \beta_{4,j}$ = taxa-specific effect of temperature.

$\text{bet}[5,\text{spec}[i]] = \beta_{5,j}$ = taxa-specific effect of clay content of soil.

$\text{bet}[6,\text{spec}[i]] = \beta_{6,j}$ = taxa-specific effect rainfall.

$\text{bet}[7,\text{spec}[i]] = \beta_{7,j}$ = taxa-specific effect of fire.

$\mu[j]$ = The community average for the associated bet parameter.

$\tau[j]$ = Precision. Variation in the associated bet parameter across species.

$w[i]$ = Indicator variable for model reduction.

$i13[i]$ and $i00[i]$ = the duration of inundation at location i in 2013 and 2000, respectively.

$\text{metric}[i]$ = the weighted flood duration metric.

z = the weighting factor between 2013 and 2000 flood covariate.

Model code:

```
model{  
  
## THE MODEL  
  
for(i in 1:n){  
  
y[i] ~ dbern(psi[i])  
  
logit(psi[i]) <- mubet[i] + epi[i]  
  
epi[i] ~ dnorm(0,taub[spec[i]])  
  
mubet[i] <- bet[1,spec[i]] + bet[2,spec[i]]*(metric[i]) + bet[3,spec[i]]*(metric[i])^2 +  
          bet[4,spec[i]]*temp[i] + bet[5,spec[i]]*clay[i] +  
          bet[6,spec[i]]*rain[i] + bet[7,spec[i]]*fire[i]  
  
metric[i] <- ((1-z)*i13[i])+(z*i00[i])  
  
}
```

```
}
```

```
## HYPERDISTRIBUTIONS
```

```
for(j in 1:7){
```

```
for(i in 1:nspec){
```

```
b[j,i] ~ dnorm(mu[j],tau[j])
```

```
}
```

```
}
```

```
## PRIORS
```

```
mu[1] ~ dt(0,pow(1.566267,-2),7.63179)
```

```
tau[1] <- pow(sig[1],-2)
```

```
sig[1] ~ dt(0,2/(.3^2),2) T(0,10)
```

```
for(j in 2:7){
```

```
mu[j] ~ dt(0,pow(1.566267,-2),7.63179)
```

```
tau[j] <- pow(sig[j],-2)
```

```
sig[j] ~ dt(0,2/(.3^2),2) T(0,10)
```

```
}
```

```
## MODEL SELECTION
```

```
for(j in 1:nspec){
```

```
taub[j] <- pow(sigb[j],-2)
```

```
sigb[j] <- randmu#~ dnorm(randmu,randtau)
```

```
bet[1,j] <- b[1,j]
```

```
bet[2,j] <- (w[1]==2)*b[2,j] + (w[1]==3)*mu[2]
```

```
bet[3,j] <- (w[2]==2)*b[3,j] + (w[2]==3)*mu[3]
```

```
bet[4,j] <- (w[3]==2)*b[4,j] + (w[3]==3)*mu[4]
bet[5,j] <- (w[4]==2)*b[5,j] + (w[4]==3)*mu[5]
bet[6,j] <- (w[5]==2)*b[6,j] + (w[5]==3)*mu[6]
bet[7,j] <- (w[6]==2)*b[7,j] + (w[6]==3)*mu[7]
}
for(i in 1:7){w[i]~ dcat(pi[i])
}
randtau <- pow(randsig,-2)
randsig ~ dt(0,2/(.6^2),2) T(0,10)
randmu ~ dt(0,2/(.6^2),2) T(0,10)
z ~ dunif(0,1)

}
```

Supplementary 2.3. Model fit evaluation and reduction results.

Both model error structures produced equivalent ability to predict the data, which was an 0.82 probability of predicting the correct occurrence and non-occurrence state. Because these error structures produce equivalent predictions, model selection theory would suggest that the optimal model choice is the simpler of the error structures, i.e. the Bernoulli error structure. This choice was supported by DIC which indicated the Bernoulli error structure was the most parsimonious model structure. The Bernoulli model had a DIC that was >230 likelihood points lower than the Logit-Normal error structure, indicated full support (Table S#).

Table S.2.1. Model fit statistics for two model error structures.

Metric	Bernoulli	Logit-Normal Bernoulli
Zero	0.89	0.89
Non-zero	0.39	0.39
All	0.82	0.82
DIC	1006.99	1241.27
Deviance	908.32	890.45

The Stochastic Search Variable Selection model reduction procedure indicated the greatest support for the main effect of inundation (B2), which had a total inclusion probability of 1.00 and 1.00 probability of being variable among species. The covariate with the second highest support was the quadrated effect of inundation (B3); however, there was high structural uncertainty as to whether these effects varied among species. The remainder of the covariate demonstrated little support by the SSVS procedure (see Table 1 in the main text).