Biological Conservation 215 (2017) 1–10

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Floodplain habitat is disproportionately important for bats in a large river basin

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ARTICLE INFO

Keywords:
Acoustics
Agriculture
Chiroptera
Community ecology
Flooding
River regulation
Water
Wetland

ABSTRACT

Floodplain ecosystems across the world have declined with river regulation and floodplain development, reducing flood frequency and extent and fragmenting flood-dependent vegetation. There is growing evidence that these changes to flooding disproportionately affect terrestrial taxa, such as bats. We compared bat activity and insect abundance across the floodplain mosaic (river, lake, vegetated wetland, floodplain forest, floodplain woodland) representing decreasing flooding histories, and two dry habitats (dry vegetation, agricultural). We replicated these habitats in each of six floodplain systems of the Murray-Darling Basin, a large semi-arid river basin (1,042,730 km^2) in south-eastern Australia. Our sites were spread across > 400,000 km^2, traversing climatic and hydrological gradients. Rivers and lakes with open water and riparian trees had greater total activity (5 times), foraging activity (14 times) and bat richness (1.5 times) than dry vegetation. Activities of all mesic bat species, as well as some widespread and arid-adapted bat species, were positively associated with floodplain habitats when compared with dry vegetation. Lowest overall total activity, foraging activity and richness were observed in dry agricultural (cropping, grazing and fallow) habitats, with two of six threatened species in our study area never recorded in agricultural habitats. Prey abundance was not correlated with bat activity or habitat. The mosaic of floodplain habitats appears to be of disproportionate value for bat communities compared to dominant land covers of agricultural and dry vegetation. Loss of floodplain habitats through continued river regulation and floodplain development are likely reduce diversity and abundance of bats that rely on floodplains for foraging and roosting. Lags in bat roost formation and forest structure mean these changes could take over a century to reverse. To sustain bat communities, we recommend increasing environmental flows to floodplains during the bat lactating season, implementing stronger protection of floodplains from river regulation and floodplain development and where possible, restoring floodplains affected by agriculture into functioning wetlands.

1. Introduction

More than 70% of the world's wetlands have been destroyed and impaired (Kingsford et al., 2016), with floodplain wetlands often the first to be lost as a result of river regulation and floodplain development (Kingsford, 2015). Aquatic and water-dependent taxa, such as microinvertebrates (Jenkins and Boulton, 2007), fish (Rayner et al., 2009), turtles (Ocock et al., 2017), frogs (Ocock et al., 2016) and water birds (Kingsford and Thomas, 2004) rely on frequent flooding and are sensitive to anthropogenic alterations of floodplain habitats. Less is known about how terrestrial fauna respond to floodplain disturbance (Mac Nally et al., 2011). However, declines in productivity due to reduced flooding and absence of shelter/nesting structures (e.g. hollow-bearing trees and fallen timber) as a result of floodplain development impact both mobile and vagile terrestrial species (Lada et al., 2007; McGinness et al., 2010). As anthropogenic climate change progresses, floodplains are likely to become increasingly important for terrestrial fauna as climate refugia (Selwood et al., 2015).

Bats are widespread mobile terrestrial predators that forage on aquatic emergent prey in wetland and floodplain environments (Fukui

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http://dx.doi.org/10.1016/j.biocon.2017.08.030
Received 24 February 2017; Received in revised form 18 August 2017; Accepted 22 August 2017
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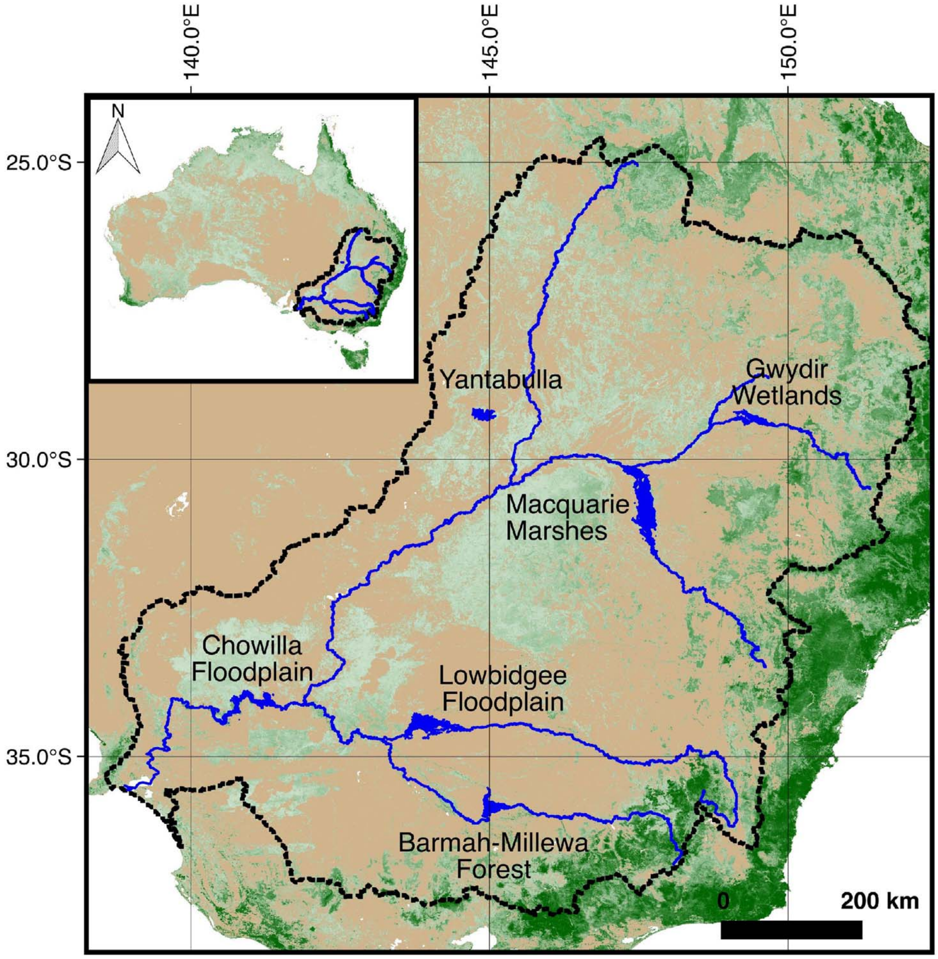

Fig. 1. Bats and insects were sampled at six floodplain systems within of the Murray-Darling Basin (black dashed line) in south-eastern Australia. Floodplain extent of the six floodplain systems and main rivers are shown in blue and degree of green shading reflects increasing canopy cover around the river from treeless (brown) to high canopy dark green (30 m resolution, Joint Remote Sensing Research Program, 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2006; Power et al., 2004) and require water to drink (Griffiths, 2013), especially when nursing young (Adams and Hayes, 2008). Despite this, few studies have investigated the importance of floodplains for bats (Monamy et al., 2013; Pereira et al., 2009). Many bat species rely on freshwater ecosystems and some bats (e.g. fish eating bats) trawl for aquatic insects and fish (Campbell, 2009). They also travel and forage along riparian corridors in dense forests (Law and Chidel, 2002; Law et al., 2011) with some bat species preferentially roosting in hollow trees within floodplains even when foraging areas are up to 10 km away (Lumsden et al., 2002). Some arid-adapted bat species have evolved techniques to cope with the threat of water loss, using torpor (decreasing body temperature and metabolic rate) (Bondarenco et al., 2013). Such species can live over 10 km from any water source (Williams and Dickman, 2004). Corresponding to these dependencies, bat species are vulnerable to changes in water regimes, pollution and climate (Jones et al., 2009) and bat species that are closely tied to water for all parts of their life cycle, are most vulnerable (Campbell, 2009).

Freshwater ecosystems are also highly productive, supporting higher abundances of insects and bats than nearby terrestrial ecosystems (Fukui et al., 2006). In floodplains, vegetation communities change across a gradient of flooding regimes, creating a range of foraging opportunities that vary temporally and spatially. This environmental variability contrasts with the more homogeneous conditions in adjacent terrestrial areas. Flooding brings nutrients from large floodplain areas, concentrating productivity in rivers and wetlands and dramatically increasing abundance and richness of insectivorous bats (Pereira et al., 2009; Rainho and Palmeirim, 2011). Productivity of foraging habitats, leading to greater abundances of insect prey, may be especially important during the breeding season when lactating bats are experiencing their greatest energetic challenges (Kurta et al., 1989). This may also be when water balance is critical for bats, due to high temperatures and water requirements for flight and lactation (Adams and Hayes, 2008). Bat activity and prey availability can decrease dramatically when river flows decline in arid systems (Hagen and Sabo, 2012, 2014).

The Murray-Darling Basin (1,042,730 km^2) in south-eastern Australia has highly variable flooding regimes, affected by river regulation (Kingsford, 2000). It provides an ideal landscape to investigate the dependency of bat communities on the mosaic of floodplain habitats, including rivers, lakes, vegetated wetlands, floodplain woodlands and forests, created by flooding regimes (Saintilan and Overton, 2010), and that contrast with terrestrial areas. The basin also has a diverse bat fauna (Law and Anderson, 1999; Lumsden and Bennett, 1995; Monamy et al., 2013; Reside and Lumsden, 2011). These floodplain habitats exist within a matrix of agricultural areas and remnant dry native vegetation. The basin is highly regulated by dams, diversions and impoundments, reducing the surface water availability by 48% (Leblanc et al., 2012), and requiring national investment to return water to rivers and floodplains in order to restore biodiversity and ecological functioning (Swirepik et al., 2016). Measurements of impacts to rivers and wetlands and subsequent restoration attempts have generally focused on aquatic taxa and riparian vegetation (Poff and Zimmerman, 2010). We investigated dependencies of bat species across a mosaic of floodplain habitats in the Murray-Darling Basin and contrasted this to terrestrial ecosystems. We predicted that frequently flooded environments would be preferred foraging habitats over dry environments. We predicted that increased foraging would be correlated with higher prey availability in frequently flooded sites, which have greater habitat

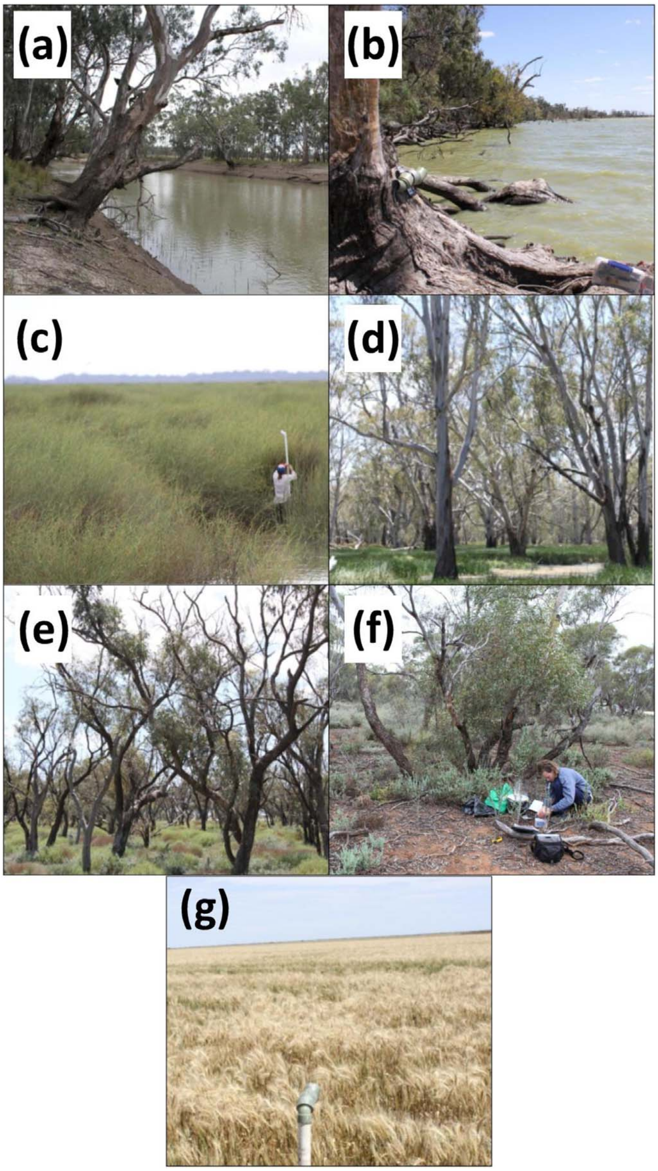

Fig. 2. Mosaic of floodplain habitat, representing the gradient of flooding, categorised into five floodplain habitats ((a) river, (b) lake, (c) vegetated wetland, (d) floodplain forest, (e) floodplain woodland) and two dry habitats ((f) dry vegetation and (g) agricultural habitat).

availability for emergent prey as well as high productivity that results in abundant terrestrial prey. We also predicted that species level associations across the mosaic of floodplain environments would vary, with water dependent and mesic-adapted bats showing strongest positive associations with floodplain habitats.

2. Materials and methods

2.1. Study area

We surveyed bats and insects within six floodplain systems of the Murray-Darling Basin in south-eastern Australia (1,042,730 km^2, 14% of the Australian continent). Each floodplain system included a mosaic of floodplain habitats as well as dry vegetation and agricultural areas around a main river system within the broader Murray-Darling basin (Figs. 1 & 2, Appendix S1). The floodplain systems varied in their river regulation history, climates and plant communities (Appendix S1). The Murray-Darling Basin has a highly variable climate both spatially and temporally. Our floodplain systems ranged from hot and arid in the north-west with annual rainfall of 344 ± 21 mm and annual temperatures of 20.0 ± 0.01 °C (Yantabulla), to relatively cool and temperate in the south-east (Barmah-Millewa Forest: 677 ± 78 mm; 13.6 ± 0.4 °C) (Appendix S2). We sampled during extensive inundation, when high surface inflows (2010 − 2011) after a prolonged drought produced the greatest flooding extent observed for ten years in the Murray-Darling Basin (Huang et al., 2014).

2.2. Survey design

We sampled the floodplain mosaic by identifying seven habitats a priori for each of the six floodplain systems of the basin, including five floodplain habitats decreasing in perenniality (the river channel (~15–100 m width); lake (> 1 ha); vegetated wetland; floodplain forest; floodplain woodland), and two dry habitats (dry vegetation and agricultural land) (Fig. 2). River channels were perennially flooded, except for within the most arid floodplain (Yantabulla), where the main river (Cuttaburra Creek) was ephemeral. Lakes and vegetated wetlands were defined as requiring annual flooding and were open (treeless) patches, either predominantly free of vegetation (lakes) or vegetated (vegetated wetland). Floodplain forest and floodplain woodland were dominated by trees, requiring flooding every 1–3 years and 2–10 years, respectively. Wetland plants that dominated vegetated wetlands included: *Muehlenbeckia florulenta*, *Phragmites australis*, *Typha domigensis* and *Bolboschoenus fluviatilis*. Floodplain trees were dominated by *Eucalyptus camaldulensis*, *E. coolabah* (river, lake, floodplain forest), and *E. largiflorens* (floodplain woodland). Dry vegetation was dominated by trees that were generally not flood dependent and included *Acacia aneura*, *E. populnea* and *E. oleosa*. Treed areas were relatively open (250 ± 32 trees per ha) with relatively low canopies (14.8 ± 1.2 m). Agricultural habitats were open (treeless) areas > 100 ha, either cropped, grazed or fallow and not regularly flooded, although sometimes irrigated. All river and lake habitats held standing water, while a third of vegetated wetland sites and 40% of floodplain forest sites had just dried recently (soil was still moist) and all floodplain woodland sites were dry or had dried recently. All dry vegetation and agricultural sites were dry and had not been recently flooded but may have been irrigated. The seven habitats accounted for most landuse types within the Murray-Darling Basin.

We sampled bats and insects, in two and one locations respectively, in each habitat in each floodplain system. There were 79 bat sites (164 nights) and 40 insect sites (77 nights); equipment failed on five bat and two insect sites. Each site was > 200 m from roads or tracks and at least three kilometres from other sites, reducing spatial autocorrelation. Dry vegetation, and agricultural sites were at least 10 km from open water. Overall, the sites sampled spanned a geographic area of > 400,000 km^2. We selected sites haphazardly, rather than randomly, due to the logistical limitations of the large study area. However, we checked for biases in our sampling by comparing important covariates for bats (tree stem density and hollow availability) across our treed sites (river, floodplain forest, floodplain woodland, dry vegetation) using analysis of variance (ANOVA). We found no evidence for differences in either stem density ($F = 0.52$, $P = 0.670$) or hollow availability ($F = 0.57$, $P = 0.637$) among habitats.

2.3. Bat and insect surveys

We surveyed bats and insects during bat lactation (Nov–Dec, 2011), given this is a period of high energetic (Kurta et al., 1989) and water (Adams and Hayes, 2008) demands for bats. We recorded echolocating bats using Anabat call recorders (Anabat II, Anabat SD1, Titley Scientific, Brendale, QLD, Australia), calibrated to the same detection distance using a bat chirper (Nevada Bat Technology, Las Vegas, NV, USA). The lactation period coincides with the Australian spring-summer, which is a relatively hot and dry season within the study area.

Ultrasonic microphones were placed 1 m above ground (or above vegetation where ground vegetation > 1 m high), protected from the weather within S-bend PVC pipes, and pointed vertically at a 45° angle toward vegetation gaps, to reduce sound attenuation from vegetation clutter (Patriquin et al., 2003). Bat recorders were programmed to record from dusk to 1 h after dawn, for 1–4 nights (2.1 ± 0.1 nights) at each site, outside full moon periods (± 3 days). We did not sample on rainy nights. We intended to sample for three nights at each site but equipment failure and site access issues prevented this.

We analysed bat calls (each file recorded by the recorders comprised a sequence of pulses and was considered a separate call), using automated call identification software Anascheme (Adams et al., 2010), with a local key identifying species or genus and a filter for bats with alternating frequencies (e.g. *Chalinolobus gouldii*). The key misclassified < 2% of calls ($n = 398$), tested against independent reference calls of species expected within the study area (Appendix S3). We created two genus groups because of call similarity: *Nyctophilus* (*Nyctophilus geoffroyi*, *N. gouldi*, *N. corbeni*) and *Mormopterus* (*M. ridei*, *M. planiceps, M. petersi*). We manually identified all *M. macropus* calls due to their similarity to *Nyctophilus* spp. calls and also manually checked all uncommon and threatened species. Feeding buzzes of bats honing in on prey were filtered, identified as sequences of short pulses with more linear structure than other calls and then edited by manually removing all calls that were not feeding buzzes (e.g. steep clutter calls). We could not discount that some buzzes were drinking calls, where water was present, given similar call structures (Griffiths, 2013). Our final bat response variables, estimated for each night, included: total activity (total number of bat calls per night including feeding buzzes); foraging activity (number of calls classified as feeding buzzes per night); bat richness (number of bat species or genera identified) and taxa activity (total activity of 14 bat taxa). Each bat taxa was also assigned to one of three groups, representing decreasing dependence on water (mesic, widespread, arid-adapted), based on ecology of the 14 bat taxa of this study (Churchill, 2009; Monamy et al., 2013).

We sampled nocturnal insects 10 min every hour, for 8 h after sunset, using a 12 V DC 8 watt insect light trap (E700, Australian Entomological Supplies Pty Ltd., Bangalow, Australia) placed > 200 m from bat recording sites, to avoid potential disturbance (Adams et al., 2005). Insects were preserved in 70% ethanol, sorted into taxonomic order and size class and counted, excluding non-flying taxa. Size classes were consistent with Lumsden and Bennett (2005) and based on the length of the insect body (0.1–2, 2.1–4, 4.1–6, 6.1–10, 10.1–14, 14.1–18, 18.1–24, > 24 mm). We calculated four univariate metrics of prey availability: total insect abundance, terrestrial insect abundance, aquatic insect abundance and insect order richness. Terrestrial insect abundance contained insect orders that were predominantly of terrestrial origin (Hymenoptera, Lepidoptera, Coleoptera, Hemiptera, Dermaptera, Orthoptera, Blattodea, Isoptera) and aquatic emergent insect abundance included orders with predominantly aquatic larval stages (Trichoptera, Ephemeroptera, Neuroptera and Plecoptera) (Lancaster and Downes, 2013). The orders Coleoptera and Hemiptera were likely to contain both terrestrial and aquatic taxa but these were not separated and therefore our abundance metrics for aquatic taxa are approximate. We calculated multivariate insect order abundance for 10 insect orders (Hymenoptera, Lepidoptera, Trichoptera, Diptera, Coleoptera, Hemiptera, Dermaptera, Orthoptera, Blattodea, Isoptera), recorded as bat prey (Law and Urquhart, 2000; Lumsden and Bennett, 2005) and sufficiently abundant (> 1%) in samples. All of the insect abundance measures were also converted to biomass by using the mean length of the size class in empirical relationships, relating insect dry biomass to insect body length for different orders (Sample et al., 1993). However, correlations between biomass and abundance were very high (e.g. total insect abundance/biomass, $R^2 = 0.92$, terrestrial insect abundance/biomass, $R^2 = 0.92$, aquatic emergent insect abundance/biomass, $R^2 = 0.95$) so only insect abundance relationships were reported.

We visually estimated open water at each site, as a percentage cover of the whole site (a 25 m by 50 m quadrat, extending 50 m in the direction that the bat call recording microphone was pointed and 12.5 m either side of the microphone). We characterised nightly fluctuations in temperature using maximum nightly temperature from the Bureau of Meteorology (Bureau of Meteorology, 2014). Finally, to account for climatic differences across floodplain systems, we recorded annual temperature, annual rainfall and annual runoff from historical data (1921–1995) at the sub-catchment level for each site (Stein et al., 2011).

2.4. Data analyses

To test for a relationship between bat habitat use (total activity, foraging activity) and habitat, we fitted negative binomial generalised mixed effects models (Warton et al., 2016). Habitat (river, lake, vegetated wetland, floodplain forest, floodplain woodland, dry vegetation and agricultural) was the fixed factor and site and floodplain system were random factors using the R-package *glmmADMB* v0.8.3.2 (Skaug et al., 2015). A second set of negative binomial mixed effects models were fitted with bat prey abundance (total insect abundance, terrestrial insect abundance, aquatic insect abundance) as the response variables with the same predictor variables. As the two richness response variables (bat richness and insect order richness) were normally distributed, we used linear mixed effects models within the lme4 v1.1-13 (Bates et al., 2017) and lmerTest v2.0-33 (Kuznetsova et al., 2016) packages to fit these models. We checked for correlation among all of our response variables using the Pearson's correlation coefficient.

We used a forward-stepwise model selection procedure to check whether nightly fluctuations in temperature (maximum nightly temperature), climate (annual rainfall, temperature and runoff) or open water (percentage open water) added additional explanatory power to the base models (models containing only habitat as fixed variable). We added each variable one at a time to form a set of candidate models, comparing models using the BIC and retaining the variable that resulted in the best fitting (lowest BIC) model. We then compared this model with the null model (the model without the variable in question) using ANOVA to check whether addition of the variable significantly improved model fit. This process was continued along the forward selection path until additional variables no longer improved model fit ($P < 0.008$). We used the Bonferroni correction to adjust our significance threshold from $P < 0.05$ to $P < 0.008$, to account for multiple testing among the 6 predictor variables (Rice, 1989). After each new variable was added to the model, highly correlated variables ($R^2 > 0.7$) were removed from the selection pool to reduce collinearity, which distorts model estimation (Dormann et al., 2013). The list of all models, their BIC, ΔBIC (compared with the base models) and ANOVA results in Appendix S4.

Once the final model was selected, we assessed goodness-of-fit using Dunn-Smyth residual plots (Dunn and Smyth, 1996). In these plots, we looked for fan shapes and extreme residual values that might indicate unaccounted for overdispersion or a violation of distributional assumptions (Warton et al., 2016). Finally, we added number of sampling nights as a covariate, but as it was not significant for any of the response variables it was removed from the final models. We tested the significance of each explanatory variable using the X^2 statistic for categorical variables and the z statistic for continuous variables and levels within categorical variables. The resulting most parsimonious models were reported with dry vegetation as the reference category to best compare relative importance of floodplain habitats. We calculated the proportion of variance explained by the fixed variables in the model (marginal R^2) and by both fixed and random variables (conditional R^2) (Nakagawa and Schielzeth, 2013) using scripts for models of the negative binomial family provided in Nakagawa and Schielzeth (2017).

We also examined relationships between habitat and community-level (multivariate) response variables (bat taxa activity and insect order abundance), using a model-based analysis of multivariate abundance data in the *mvabund* (v3.9.1) package (Wang et al., 2012) with the negative binomial distribution (function: *manyglm*). This technique fits separate generalised linear models to each response variable (species) with a common set of explanatory variables, and uses resampling to test hypotheses (Wang et al., 2012). We again used the negative binomial family, which is appropriate for analysis of species community data, as it works well for overdispersion and mean-variance relationships common in count data (Warton et al., 2016). Observations were summed for all nights at each site, using number of nights as an offset within the model. Significance of each variable was tested using the Likelihood Ratio Test (LRT) statistic, and 95% confidence intervals were calculated for modelled coefficients. This allowed us to identify community-level effects of habitat and to identify which taxa (bat or insect order) were likely drivers of these differences. Floodplain system was not included as a predictor, as its inclusion contributed little to models of bat habitat use and insect abundance (Tables 2 & 3). We used Dunn-Smyth residual plots and mean-variance plots to assess model fit (Wang et al., 2012). We used the R environment for statistical computing (R v3.3.1) to conduct all analyses (R Development Core Team, 2016).

3. Results

We recorded a total of 68,147 bat calls from 14 bat taxa, over 164 recording nights. On average, there were 416 ± 32 (SE) total calls per night. Of these, we identified 58% to individual taxa (one of 12 bat species or two genera), with remaining calls either fragmentary or of poor quality. Total activity and bat richness across floodplain systems broadly followed patterns in annual rainfall, temperature and runoff (Table 1; Appendix S2). The more arid floodplain systems (Yantabulla, Gwydir Wetlands, Macquarie Marshes) had lower total activity and richness but higher insect abundance and order richness compared to more mesic floodplains (Barmah-Millewa Forest, Lowbidgee Floodplain, Chowilla Floodplain) (Appendix S2). Among the response variables, total and foraging activity were correlated ($R^2 = 0.75$), and total insect and terrestrial insect abundance were highly correlated ($R^2 = 0.95$), however bats and insects were not correlated (all measures $R^2 < 0.20$).

Despite variability across floodplain systems, all measures of bat habitat use differed significantly among habitats, with greater activity in more frequently flooded habitats (total activity: $X^2 = 48.64$, $P < 0.001$; foraging activity: $X^2 = 44.05$, $P < 0.001$; bat richness: $X^2 = 13.28$, $P < 0.001$; Table 2). The wettest habitats (river and lake) had greater total activity (5 times), foraging activity (14 times) and bat richness (1.5 times) compared to dry vegetation habitats (Table 2, Fig. 3). However in infrequently flooded floodplain woodland, bat habitat use was similar to dry vegetation (Fig. 3). Agricultural habitats supported the lowest total bat activity, bat foraging activity and bat richness with nine times and 19 times less total and foraging activity, respectively, than the wettest (river and lake) habitats (Fig. 3). Bat richness roughly doubled from ~ 4 species recorded nightly in agricultural habitats to ~ 8 species recorded in lakes (Fig. 3).

Habitat did not significantly improve the models for any of our insect abundance or richness variables. These included: Aquatic insect abundance ($X^2 = 12.65$, $P = 0.049$), terrestrial insect abundance ($X^2 = 3.85$, $P = 0.698$), total insect abundance ($X^2 = 5.50$, $P = 0.482$) and insect order richness ($X^2 = 12.81$, $P = 0.046$). All measures of insect abundance and richness except aquatic insect abundance were related to fluctuations in temperature, increasing with maximum nightly temperature (terrestrial insect abundance: $z = 5.86$, $P < 0.001$; total insect abundance: $z = 4.49$, $P < 0.001$; insect order richness: $t = 3.64$, $P = 0.001$; Table 3; Appendix S4). The model of aquatic insect abundance fit poorly, as habitat only explained 7% of the modelled variability (Table 3). Insect community composition did not vary significantly across habitats ($\text{LRT} = 109.7$, $P = 0.414$, Appendix S5). No measures of bat habitat use (total activity or foraging activity) were related to any measures of insect abundance (total, aquatic emergent and terrestrial insect abundance, taxa-specific prey measures) (Appendix S6).

Bat community composition differed across habitats ($\text{LRT} = 261.3$, $P = 0.001$; Fig. 4). All bat species were recorded in all habitats except two threatened species. *Myotis macropus* (mesic) was not recorded in agricultural habitats, dry vegetation or floodplain woodland, and *Chalinolobus picatus* (arid-adapted) was not recorded in agricultural habitats (Fig. 4, Appendix S7). Five bat species were negatively associated with agricultural compared to dry habitats and no species were positively associated with agricultural or dry vegetation compared to floodplain (Fig. 4). In contrast, nine species were positively associated with floodplain habitats including all mesic species, three widespread species and two arid-adapted species (Fig. 4). Of six threatened species (Appendix S7), two were positively associated with floodplain habitats and three negatively associated with agricultural habitats (Fig. 4). There was support for increasing bat habitat use across the flooding gradient as eight species were positively associated with rivers, six with lakes, seven with vegetated wetland, four with floodplain forests and only two species positively associated with floodplain woodland (Fig. 4).

4. Discussion

A key finding of our study was that more frequently flooded habitats supported greater bat (total and foraging) activity and bat richness than

Table 1
Mean (± SE) activity (calls per night) for 14 bat taxa and total activity and foraging activity, recorded on six floodplain systems within the Murray-Darling Basin, south-eastern Australia (see Fig. 1).

Species	Yantabulla	Macquarie Marshes	Gwydir Wetlands	Chowilla Floodplain	Lowbidgee Floodplain	Barmah-Millewa Forest
Myotis macropus	0	0.33 ± 0.29	0	0.04 ± 0.04	0.18 ± 0.14	3.58 ± 2.33
Vespadelus darlingtoni	0	0	0	3.24 ± 1.23	1.79 ± 1.58	46.14 ± 24.32
Vespadelus regulus	0	0	0	123.45 ± 56.91	97.17 ± 48.31	27.6 ± 13.52
Chalinolobus morio	0	0	0.06 ± 0.04	22.89 ± 7.36	4.68 ± 1.73	2.74 ± 1.42
Vespadelus vulturnus	0	20.58 ± 9.31	37.35 ± 10.75	3.68 ± 0.97	32.68 ± 12.71	105.67 ± 50.09
Mormopterus lumsdenae	0	0	1.12 ± 0.41	0	0	0
Austronomus australis	0.09 ± 0.05	0.21 ± 0.1	0.18 ± 0.09	0.73 ± 0.24	37.26 ± 17.62	12.54 ± 5.38
Saccolaimus flaviventris	11.28 ± 4.28	3.94 ± 1.38	7.77 ± 2.61	0	0.17 ± 0.08	0.19 ± 0.12
Nyctophilus spp.	3.49 ± 1.55	14.29 ± 8.88	2.85 ± 1.37	2.71 ± 2.21	6.4 ± 4.24	4.67 ± 1.65
Chalinolobus gouldii	14.76 ± 7.61	36.38 ± 14.59	5.26 ± 2.53	33.45 ± 15.51	61.02 ± 21.31	20 ± 6.14
Mormopterus spp.	24.06 ± 10.11	40.43 ± 11.45	142.08 ± 38.91	82.2 ± 19.85	63.6 ± 17.71	60.67 ± 23.65
Chalinolobus picatus	8.95 ± 6.97	0.56 ± 0.26	0	0.25 ± 0.16	0	0
Scotorepens greyii	84.56 ± 24.75	31.57 ± 8.8	27.96 ± 11.51	0.43 ± 0.16	1.29 ± 0.51	0
Scotorepens balstoni	1.05 ± 0.38	4.88 ± 2.6	10.48 ± 6.62	0.63 ± 0.28	2.73 ± 1.22	1.24 ± 0.54
Total activity	259.01 ± 77.24	374.71 ± 84.85	382.81 ± 98.13	430.74 ± 105.12	540.31 ± 165.08	476 ± 132.04
Foraging activity	9.88 ± 4.99	6.83 ± 2.54	12.74 ± 4.44	26.63 ± 8.99	33.06 ± 15	30.59 ± 13.75

Table 2
Summaries of fitted mixed effects models relating total activity (calls per night), foraging activity (buzzes per night) (generalised linear: negative binomial) and bat richness (linear) to significant predictors and habitats. The reference category (intercept) for habitat was dry vegetation. Standard deviations (SD) are shown for random factors (site and floodplain system) and standard errors (SE) for fixed factors. Variance gives the amount of variability within random intercepts for different sites and floodplain systems. The test statistic (TS) was the z statistic for generalised linear mixed effects models (total and foraging activity) and the t statistic for linear mixed effects models (bat richness). Marginal R^2 (R^2M) estimates the variance explained for the fixed effects in each model (without the random effects), while Conditional R^2 (R^2C) estimate the variance explained for both fixed and random effects.

Response (R^2M/R^2C)	Predictors	Variance	Coefficient	SD/SE	TS	P
Total activity	Site	0.520		0.721		
(0.42/0.81)	Floodplain system	< 0.001		< 0.001		
	Intercept		4.87	0.25	19.37	< 0.001
	Agricultural habitat		− 0.64	0.35	− 1.82	0.068
	Floodplain woodland		0.29	0.34	0.85	0.396
	Floodplain forest		0.85	0.35	2.46	0.014
	Vegetated wetland		0.97	0.34	2.83	0.005
	Lake		1.56	0.35	4.45	< 0.001
	River		1.63	0.35	4.7	< 0.001
Foraging activity	Site	1.478		1.122		
(0.39/0.77)	Floodplain system	< 0.001		< 0.001		
	Intercept		0.46	0.48	0.97	0.33
	Agricultural habitat		− 0.34	0.68	− 0.5	0.618
	Floodplain woodland		0.2	0.64	0.32	0.752
	Floodplain forest		1.19	0.63	1.88	0.059
	Vegetated wetland		2.25	0.62	3.63	< 0.001
	Lake		2.92	0.63	4.63	< 0.001
	River		2.71	0.63	4.33	< 0.001
Bat richness	Site	2.35		1.53		
(0.33/0.72)	Floodplain system	< 0.001		< 0.001		
	Intercept		5.26	0.56	9.32	< 0.001
	Agricultural habitat		− 0.93	0.79	− 1.17	0.245
	Floodplain woodland		0.54	0.77	0.7	0.488
	Floodplain forest		1.68	0.77	2.18	0.033
	Vegetated wetland		1.26	0.77	1.64	0.106
	Lake		2.38	0.78	3.05	0.003
	River		2.09	0.78	2.68	0.009
	Annual temperature		− 0.8	0.21	− 3.87	< 0.001

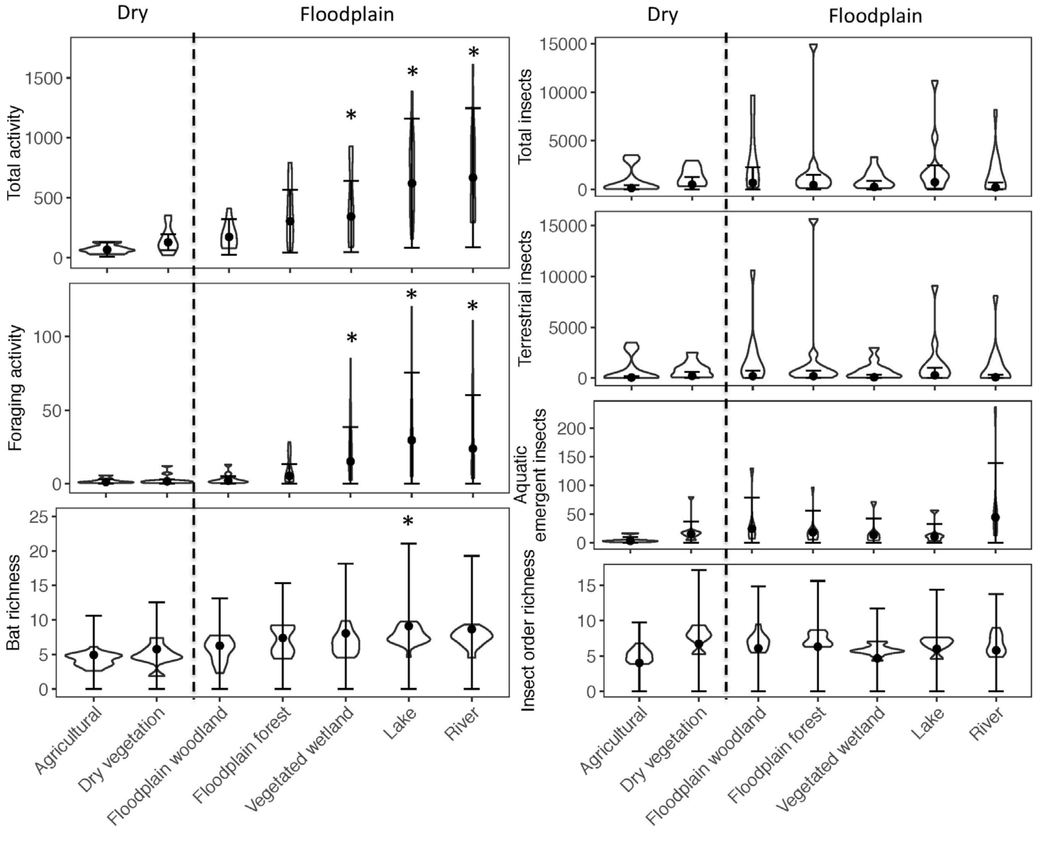

Fig. 3. Violin plots of fitted means (± 95% CI) of bat habitat use total activity (calls night^{-1}), foraging activity (no. feeding buzzes night^{-1}), bat richness (number of bat taxa recorded night^{-1}), bat prey abundance (total insects, terrestrial insects, aquatic insects) and insect order richness, across a mosaic of five floodplain (floodplain woodland, floodplain forest, vegetated wetland, lake, river) and two dry habitats (agricultural, dry vegetation). "Violins" show probability density at different values of the response variables. Asterisks indicate floodplain habitats where the response variable was significantly different from dry vegetation.

Table 3
Summaries of fitted mixed effects models relating total insect, terrestrial insect and aquatic emergent insect abundance (generalised linear: negative binomial) and insect order richness (linear) to significant predictors and habitats. The reference category (intercept) for habitat was dry vegetation. Standard deviations (SD) are shown for random factors (site and floodplain system) and standard errors (SE) for fixed factors. Variance gives the amount of variability within random intercepts for different sites and floodplain systems. The test statistic (TS) was the z statistic for generalised linear mixed effects models (total, terrestrial and aquatic emergent insect) and the t statistic for linear mixed effects models (insect order richness). Marginal R^2 (R^2M) estimates the variance explained for the fixed effects in each model (without the random effects), while Conditional R^2 (R^2C) estimate the variance explained for both fixed and random effects.

Response (R^2M/R^2C)	Predictors	Variance	Coefficient	SD/SE	TS	P
Insect order richness	Site	0.834		0.914		
(0.30/0.51)	Floodplain system	0.412		0.642		
	Intercept		7.51	0.75	10.07	< 0.001
	Agricultural		− 2.46	0.92	− 2.69	0.012
	Floodplain woodland		− 0.41	0.94	− 0.43	0.669
	Floodplain forest		− 0.17	0.94	− 0.18	0.856
	Vegetated wetland		− 1.96	0.94	− 2.08	0.045
	Lake		− 0.81	0.94	− 0.86	0.395
	River		− 0.7	0.92	− 0.76	0.453
	Max nightly temperature		1.02	0.28	3.64	0.002
Total insects	Site	1.401		1.184		
(0.29/0.65)	Floodplain system	0.657		0.811		
	Intercept		7.09	0.75	9.52	< 0.001
	Agricultural		− 1.10	0.90	− 1.22	0.220
	Floodplain woodland		0.59	0.91	0.65	0.520
	Floodplain forest		0.16	0.90	0.17	0.860
	Vegetated wetland		− 0.58	0.91	− 0.64	0.520
	Lake		0.29	0.90	0.32	0.750
	River		− 0.62	0.91	− 0.67	0.500
	Max nightly temperature		1.18	0.26	4.49	< 0.001
Terrestrial insects	Site	1.704		1.305		
(0.34/0.75)	Floodplain system	1.523		1.234		
	Intercept		6.58	0.88	7.50	< 0.001
	Agricultural		− 0.98	0.96	− 1.02	0.310
	Floodplain woodland		0.29	0.98	0.30	0.760
	Floodplain forest		0.30	0.97	0.31	0.750
	Vegetated wetland		− 0.78	0.98	− 0.80	0.420
	Lake		0.12	0.97	0.13	0.900
	River		− 0.57	0.97	− 0.59	0.560
	Max nightly temperature		1.59	0.27	5.86	< 0.001
Aquatic emergent insects	Site	< 0.001		< 0.001		
(0.07/0.17)	Floodplain system	1.073		1.036		
	Intercept		2.71	0.73	3.7	< 0.001
	Agricultural		− 1.58	0.84	− 1.88	0.061
	Floodplain woodland		0.49	0.83	0.58	0.559
	Floodplain forest		0.19	0.79	0.24	0.812
	Vegetated wetland		− 0.12	0.81	− 0.14	0.886
	Lake		− 0.35	0.76	− 0.46	0.647
	River		1.09	0.77	1.4	0.161

dry habitats across a large river basin (Table 2, Fig. 3). Conversely, agricultural habitats had the lowest bat activity and richness of all habitats (Table 2, Fig. 3). These trends were robust to variable climatic conditions across the basin: bat activity and richness peaked where annual rainfall and runoff were high and annual temperatures were low (Appendix S2). However, insect abundance did not vary with habitat (Table 3, Appendix S5) and no measures of insect abundance including measures of prey abundance specific to bat species, were found to be drivers of bat activity (Appendix S6).

Habitats with open water sources (lakes and rivers) supported the highest bat activity and richness (Table 2, Fig. 3), consistent with other studies across the world (Korine et al., 2016; Salvarina, 2016). Bats use echolocation to detect smooth water surfaces for drinking (Greif and Siemers, 2010) and water surfaces larger than 0.5 m wide and 15 m long attract the greatest number of bat species including large, less manoeuvrable species (Razgour et al., 2010; Tuttle et al., 2006). This requirement to drink may partly explain high levels of habitat use at rivers and lakes. Riparian vegetation, alongside open water foraging and drinking areas (e.g. rivers and lakes) also probably provides high quality foraging “edges” for bats (Gonsalves et al., 2012).

As expected, all mesic bat species associated positively with floodplain habitats (Fig. 4) but so did three widespread and two arid species, including three threatened species/groups (Fig. 3). Arid-adapted bat species could move into floodplain mosaics to capitalise on productivity “booms” of flooding (Bunn et al., 2006), feeding on aquatic emergent insects during periods of high energy requirement (e.g. lactation). The floodplain trees probably also attracted bats, such as *N. geoffroyi* and *C. gouldii,* to roost in hollows (Lumsden et al., 2002). While mean activity levels within different floodplain habitats varied between species, further work is needed to determine whether species partition floodplain habitats according to preferences for different structures (Blakey et al., 2016) or prey. Selection of habitat by bats in floodplains is likely to not only be influenced by foraging habitat quality, but also roost availability (Lumsden et al., 2002), predation risk (Lima and O'Keefe, 2013), prey sources (Arrizabalaga-Escudero et al., 2015) and floodplain phase (Pereira et al., 2009). This means that multiple habitat types may be used across different seasons or even over the course of a night's foraging (Lumsden et al., 2002). Floodplains with perennial water are likely to be especially important during drought phase, which can be common in semi-arid environments. For these reasons, further studies tracking movements of individual bats and spanning longer time periods are needed to elucidate the complexities of bat floodplain habitat use.

Our lack of relationship between insects and habitat types or insects and bats may be the result of insect super abundance from extensive flooding, reflected in nightly insect biomass > 10 times that recorded in other Australian light-trapping studies (Gonsalves et al., 2013; Scanlon and Petit, 2007; Threlfall et al., 2012). Our temporal replication was limited: 1–4 nights per site during one maternity season, so

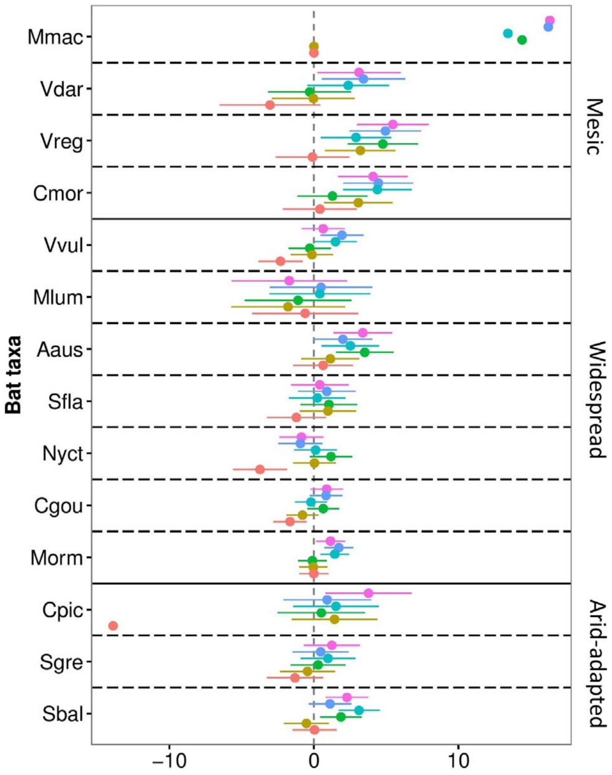

Fig. 4. Coefficient estimates (± 95% CI) from fitted multivariate generalised linear models, relating positive or negative responses in bat taxa activity (total activity of 14 bat taxa) to five floodplain habitats (purple: river, blue: lake, turquoise: vegetated wetland, green: floodplain forest, and brown: floodplain woodland) and one dry habitat (red: agricultural). The other dry habitat (dry vegetation) was the reference category, with coefficients representing comparisons with dry vegetation. Coefficients that crossed zero were not significantly different from the reference category. Confidence intervals were not calculated for coefficients where zero activity was recorded (Cpic – agricultural habitat) or where the reference category had zero activity (Mmac). Horizontal dashed lines separate bat taxa and solid lines separate water dependence categories for bats (mesic, widespread, arid-adapted). Bat taxa were arranged in predicted decreasing water dependency: *Myotis macropus* (Mmac), *Vespadelus darlingtoni* (Vdar), *Vespadelus regulus* (Vreg), *Chalinolobus morio* (Cmor), *Vespadelus vulturnus* (Vvul), *Mormopterus lumsdenae* (Mlum), *Austronomus australis* (Aaus), *Saccolaimus flaviventris* (Sfla), *Nyctophilus* spp. (Nyct), *Chalinolobus gouldii* (Cgou), *Mormopterus* spp. (Morm), *Chalinolobus picatus* (Cpic), *Scotorepens greyii* (Sgre), *Scotorepens balstoni* (Sbal). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fluctuations of insect abundance between nights with changing temperature (Table 3) may have obscured habitat relationships and decoupled the insect-bat relationship. As our study was conducted during a period of extensive inundation, we suspect that during dry periods, the importance of wet habitats for bats and insects would likely increase as emergent aquatic insects generally concentrate around water sources in drying environments (Hagen and Sabo, 2012). Further studies should investigate prey habitat during dry phases, as this may differ from bat habitat (Arrizabalaga-Escudero et al., 2015). Ideally, orders that contain both aquatic and terrestrial taxa (e.g. Hemiptera, Coleoptera and Diptera) should be separated in future studies.

4.1. Conservation implications

Clearly, there are implications from our findings for the effects of river regulation (reduction and alteration of flooding) and floodplain development (wetland loss through vegetation clearing and agriculture) on bat communities. Regulation of rivers reduces wetland extent and flooding frequency (Kingsford et al., 2016) causing dieback of floodplain forests (Cunningham et al., 2009) and reducing abundance of both aquatic and terrestrial insects (Jonsson et al., 2013). Bat activity and prey availability decline dramatically during periods of lowered river flows in arid systems (Hagen and Sabo, 2012). The Murray-Darling Basin is intensely regulated, with 248 large dams with a storage capacity of 125% annual runoff (Finlayson et al., 2013). We predict that this regulation adversely affects bat communities, due to the strong positive associations between bats and floodplain habitats, which are likely to be even stronger during periods of low flow.

Floodplain development, through the clearing of trees and disconnection of floodplain habitats (Steinfeld and Kingsford, 2013) is likely to negatively affect bat communities in the Murray-Darling Basin (Figs. 3 & 4) as it has in other world floodplains, like the Pantanal in Brazil (Alho et al., 2011). Floodplain development reduces available tree roosts (Lentini et al., 2012), foraging habitat (e.g. edges and clutter), prey abundance (Hendrickx et al., 2007) and potentially increases exposure to predators (Lima and O'Keefe, 2013). This damage continues with 70,000 ha of floodplain mosaic replaced by crops in 1997–2011 in the Gwydir Wetlands (Eco Logical Australia, 2011), a pattern reflected elsewhere in the world (Coleman et al., 2008). Such clearing may continue, as only 10.8% of floodplain wetlands in Australia are within protected areas, even though they are the most extensive wetland type in the country (55%) (Bino et al., 2016). It may take > 75 years and potentially up to 150 years for floodplain mosaics to be restored from agricultural landuse to re-establish habitat resources for insectivorous bats (Cunningham et al., 2015). Unless floodplains are protected from further clearing, bat diversity and abundance are likely to decline. Such declines in bat communities may also adversely affect surrounding agriculture, as bats provide ecosystem services in the form of insect pest regulation, increasing crop yield and decreasing pesticide costs across the globe (Kunz et al., 2011).

These effects of river regulation and floodplain development on floodplain mosaics and bat communities will be exacerbated with continuing anthropogenic climate change (Jenkins et al., 2011; Kingsford, 2011). Surface water availability is projected to decrease by a further 11% by 2030, with increased duration between beneficial floods more than doubling for 60% of wetlands in the basin across the Murray-Darling Basin (Leblanc et al., 2012). This may lead to contraction of populations of bats to floodplain mosaics (Fig. 4). Projected temperature increases range from 0.8 °C in the south to 1.1 °C in the north-western part of the Murray-Darling by 2030 (Chiew et al., 2008). These temperature increases could also reduce the number of bat species using floodplains as bat richness declined with annual temperature (Table 2).

Floodplain habitats were disproportionately important for bats compared to adjoining dry and agricultural environments for bat communities. This means that bats have joined the growing list of taxa likely to be affected by river regulation (Ballinger et al., 2005; Kingsford and Thomas, 2004; Lada et al., 2007; Ocock et al., 2016; Rayner et al., 2009; Selwood et al., 2015). Floodplain bat conservation will increasingly depend on environmental water allocations and restoration of wetlands cleared for agriculture. Priority sites are primarily open water with riparian vegetation around water margins, including canopy trees. We recommend reinstating flooding regimes in floodplain environments during the bat lactating season and preferably into the season when juvenile bats begin to fly (September–January). Also, in areas where floodplains are heavily fragmented (e.g. Gwydir Wetlands), agricultural areas that increase floodplain connectivity should be restored to functioning floodplain vegetation, cognisant of the limited restoration potential given intense cultivation histories (Dawson et al., 2016). To protect the mosaic of floodplain vegetation and thus habitat types, effort should be made to restore natural flooding regimes in floodplains (Rogers and Ralph, 2010). Finally, legal protection of remaining floodplain areas should be urgently sought, both in Australia and elsewhere as the future of the world's floodplains remains tenuous (Kingsford, 2015).

Acknowledgements

We thank Sylvia Hay, Kim Jenkins and Kat J. Bormann for improving this manuscript. Andrew Letten provided code for Fig. 4. Jane Humphries, Tim O'Kelly, Michael Mulholland, Narelle Jones, Simon Frankel, Deb and Paul Kaluder and Garry and Leanne Hall provided invaluable local expertise and on-ground support. Luke Hogan, Greg Ford and Pia Lentini generously donated reference calls to test our key and Greg Ford and Terry Reardon supplied expert assistance on call identification. Lindy Lumsden and Matina Kalcounis-Rueppell provided insightful comments on the first draft. Finally, thanks to all our volunteers for their field and lab assistance, with an extra special thank you to Liz Cameron, our Insect Lab Manager. RTK acknowledges support from the Australian Research Council Linkage Project 481 (LP0884160). This is Contribution No. 566 of The Institute for Bird Populations.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.08.030.

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