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Research Article

Importance of wetlands to bats on a dry continent: a review and meta-analysis

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Abstract

Australia has diverse landscapes ranging from wet tropical regions in the North to temperate regions in the South and a vast arid interior. This variety has given rise to not only a speciose bat fauna, but also a variety of wetland ecosystems. The relationship between bats and wetlands is influenced by a range of environmental gradients including: aridity and climate variability, hydrological, structural, productivity and salinity. However, little is known about how these gradients influence bats in Australian wetland systems. Our aim was to determine whether wetlands were important for Australia's bat communities, identify the environmental gradients influencing this importance, and review the threats to wetland bat communities combining a review and meta-analysis. We reviewed the literature on bats within wetland ecosystems in six ecoregions (arid, semi-arid floodplain, temperate, tropics, estuarine/saline and urban) in Australia. We used a meta-analysis to estimate relative wetland importance across ecoregions by calculating the effect size of the difference in bat activity between 43 paired wet and dry habitats. Bats were significantly more active in wet than surrounding dry habitats in arid and semi-arid floodplain. Urban wetlands also hosted greater bat activity than surrounding dry areas in 4 out of 7 sites. Wetlands were generally less important for bats in warm, wet tropical areas, and more important for bats in dry landscapes where landscape woody cover and productivity were low. Relative to dry areas within each region assessed, wetlands were most important for bats in semi-arid floodplain and urban regions. These regions are also under greatest threats from vegetation clearing, modification of flow regimes, development pressures, pollution and climate change.

Introduction

Australia is the flattest and driest inhabited continent (Orians and Milewski, 2007) where rainfall is extremely variable, more so than other countries with similar climates (Nicholls et al., 1997). Arid lands make up 77.8% of the continent (Peel et al., 2007) and soils are relatively old and unproductive (Orians and Milewski, 2007). Air temperature is also highly variable; for example, Australia has a higher mean annual daily temperature range (DTR) than the European and Asian continents within similar climate regions, though generally lower DTR than North America (Peel et al., 2004). Inter-annual phenomena like El Niño Southern Oscillation (ENSO) and the Indian Ocean Dipole influence Australia's variable climate with increased variability projected with anthropogenic climate change (Hughes, 2003). This variability drives the areal extent, inundation timing and nutrient loads of wetlands across the Australian continent, creating a diversity of wetland types across nearly 58 million ha of wetlands (7.5% of the continental area) (Finlayson et al., 2013). Broad wetland types include lotic (e.g. rivers), lentic (e.g. lakes, floodplains, swamps), marine wetlands and human-made wetlands (Finlayson et al., 2013). This combination of uncluttered flight space and high prey abundance provides high quality bat foraging habitat (Salvarina, 2016).

Australia's variable landscape supports a moderately speciose diversity of bats (79 species from 9 families) (Reardon et al., 2015) compared to North America (49 species) (Harvey et al., 2011) and Europe (51 species) (Dietz et al., 2007), though less than the Neotropics (288 species) where the world's greatest bat diversity occurs (Mickleburgh et al., 2002). However, the majority of research on bats and wetlands has been in Europe (47%) and North America (32%), with only 5% of studies from the Australian continent (Salvarina, 2016). The use of wetlands by bats largely depends on the availability of three key resources: roost habitat, foraging habitat (and prey) and drinking water (Korine et al., 2016). Australian bats range in their water dependency, from species that occur >10 km from water (Williams and Dickman, 2004), to Australia's only fishing bat, *Myotis macropus*, that depends on water for all parts of its lifecycle and forages from the water surface on insects and small fish (Campbell, 2007; Robson, 1984). Relationships between bats and wetland resources vary in relation to environmental gradients across the Australian continent including aridity and climate variabil-

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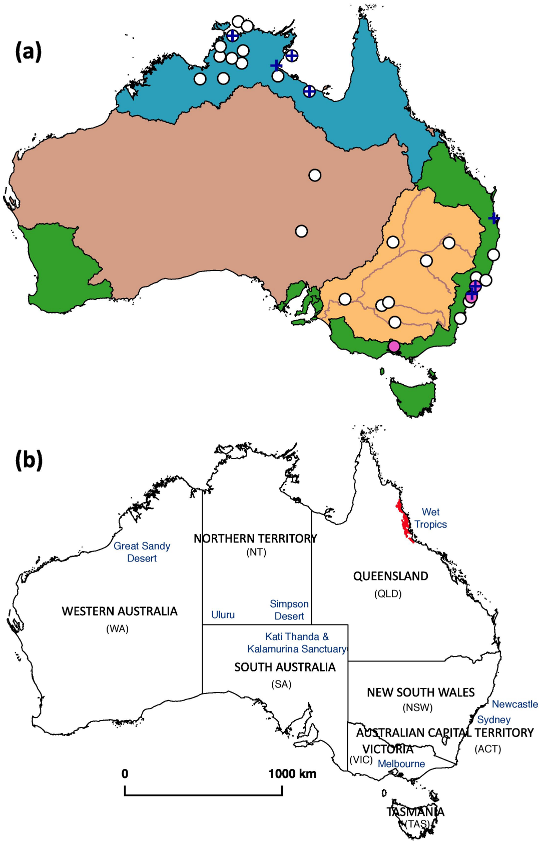

Figure 1 – Distribution of sites (a) used for meta-analysis (white circles) across the six ecoregions: arid (brown), semi-arid floodplain (orange), temperate (green), tropics (blue), wet tropics are red in (b), estuarine/saline (blue crosses) and urban (pink circles). Major rivers of the semi-arid floodplain, the Murray-Darling Basin, are shown with brown lines. States and territories (capitals with acronyms) and place names (blue) mentioned in this study are also shown (b). Studies included: Law (*unpubl. data*); Law and Chidel (2002); Williams and Dickman (2004); Milne et al. (2005); Lloyd et al. (2006); Threlfall et al. (2011); Barden (2012); Belcher et al. (2013); Wilson (2013); Broken-Brow (2013); Gonsalves et al. (2013a); McConville et al. (2014a,b); Clarke-wood et al. (2016); Straka et al. (2016a); Blakey et al. (2017).

ity, hydrological, structural, productivity and salinity gradients. All of these gradients are also influenced by anthropogenic disturbance.

Purpose of review and meta-analysis

The aim of this review and meta-analysis was to assess the importance of Australia's wetlands for bat communities while identifying key environmental gradients, discussing differences in wetland importance across six ecoregions and reviewing major threats to wetland bat communities. We focussed on echolocating bats, constituting most (86% of species) of Australia's bat diversity. We made three predictions about the influence of these environmental gradients on how Australian bats interact with wetland resources: 1) due to the increased availability of three key resources (roosting habitat, foraging habitat/prey and drinking water) in wetlands as compared to dry habitats, overall bat activity in wet habitats should be greater on average than in dry habitats; 2) the relative importance of wetlands to bats (effect size) should increase with increasing aridity, though this relationship may reach a threshold, after which the importance may decline due to a lower overall bat diversity in very arid conditions; 3) the relative importance of wetlands to bats will increase in increasingly modified habitats, reflecting a greater difference between availability of roosting, foraging and drinking resources between wetlands and surrounding modified habitats.

Wetland gradients on the Australian continent

Gradients of Aridity and Climate Variability

Across a gradient of increasing aridity from temperate areas in the southeast corner of Australia to the arid centre, or from the tropical northern coasts to the drier northwestern parts of Australia, wetland environments become increasingly ephemeral due to extremely variable rainfall and high rates of evaporation (Stafford Smith and Morton, 1990). Extensive areas of wetlands may occur in some years in highly arid regions (e.g. Kati Thanda-Lake Eyre in central Australia), but these flooding events are irregular and can be short-lived (Roshier et al., 2001). The importance of wetlands to bats is likely to increase with increasing aridity because, as temperatures increase, evaporative water loss for bats will increase and water also becomes scarce in the landscape. Additionally, some bats adapted to mesic habitats are likely to be restricted to habitats close to water where they occur in semi-arid environments (Monamy et al., 2013). It is likely this will increase the activity of bats within wetlands, relative to surrounding areas, up to a threshold of aridity. Beyond this threshold, the relative importance of wetlands in the environment may decrease, as bat species that do not have the ability to tolerate long dry periods or travel long distances to reach water, due to scarcity and ephemerality of arid zone wetlands, are excluded from the species pool. In the most arid areas of Australia, this would leave a limited species pool of bats that are able to mediate water loss and variable climates through torpor (Bondarenco et al., 2013) or urine concentration (Carpenter, 1969) and may not need to drink to maintain water balance. Because of these adaptations, wetlands may be less important for bats overall in very arid areas as compared to semi-arid areas.

Importantly, even in the most arid parts of Australia, large flooding events of rivers and floodplains irregularly occur, leading to boom and bust ecology, where productivity "booms" during periods of high flow and surface inundation are separated by longer dry periods: "busts" (Kingsford et al., 1999). A variety of biota including waterbirds, frogs and small mammals take advantage of increases in stream and floodplain productivity, sparking large breeding events in many wildlife species (Letnic et al., 2005; Kingsford et al., 2010; Ocock et al., 2014). While bats are likely to track increases in productivity and prey resources (Nakano and Murakami, 2001; Hagen and Sabo, 2012), they mostly reproduce annually, rather than in response to resource availability, thus they may be unable to increase their populations in response to flow in the same way as other floodplain biota.

Hydrological gradients

Hydrological gradients affect bats and their prey through a range of variables. These include: size and depth of water body (Francl, 2008; Jackrel and Matlack, 2010) or stream (Lloyd et al., 2006), surface properties (Jackrel and Matlack, 2010; Campbell, 2011), flooding regime (Pereira et al., 2009, 2010; Hagen and Sabo, 2012), timing of inundation (Adams, 2010), flood depth (Clement and Castleberry, 2013), and connectivity of wetlands (Lookingbill et al., 2010). In arid zones, bat activity and insect abundance can plummet, as ephemeral rivers dry (Hagen and Sabo, 2012). In semi-arid zones, frequently flooded and permanently flooded environments support greater bat activity compared to dry habitats (Blakey et al., 2017). Cycles of flooding and drying can change forest structure, affecting hollow formation (Horner et al., 2010) and thus roost availability. Flooding can also inundate roost hollows, resulting in roost switching between flooding seasons (e.g. southeastern myotis *Myotis austroriparius*, Clement and Castleberry, 2013). Connectivity of wetlands is important for species with small to moderate home ranges that prefer to forage over wetlands (Lookingbill et al., 2010), especially those that require wetland foraging habitat along migration routes (Flaquer et al., 2009). Ephemeral rivers in dry-wooded landscapes also remain important as linear foraging habitat when there is no surface water (Law et al., 2011).

Diversity in Habitat Structure: Gradients of Clutter

Australian bat communities, like bats elsewhere, use a range of habitats with varying degrees of clutter, dependent on their traits, including: echolocation call, wing morphology and body size (Denzinger and Schnitzler, 2013). This diversity in adaptation to cluttered habitats can affect the size and location of wetlands used (Francl, 2008; Vindigni et al., 2009; Jackrel and Matlack, 2010). For example, large-bodied, open-space adapted bats may prefer large water bodies (Ciechanowski, 2002; Francl, 2008; Vindigni et al., 2009) and water bodies at edges of forests (Vindigni et al., 2009), while small, more manoeuvrable bats may use a range of water body sizes and shapes (Francl, 2008; Vindigni et al., 2009). This principle also holds for streams, where open-adapted species are more active in high order (larger) streams (Lloyd et al., 2006), even in dry ephemeral rivers (Law et al., 2011). Conversely, some species prefer to forage and commute within wooded areas or along edges of wooded areas (Gonsalves et al., 2012), so large expanses of open wetlands may not be optimal for some species. Surface water clutter, through ripples or vegetation, can also adversely affect bats that trawl from the water surface (Von Frenckell and Barclay, 1987; Boonman et al., 1998). Hydrological regimes influence wetland vegetation structure, by altering the density and composition of plant communities (Bren, 1992, 2005; Rogers and Ralph, 2011), adding to the complexity of the relationship of bats to vegetation structure in wetlands.

Gradients of Productivity and Nutrients

Bat activity tends to increase with landscape productivity (Threlfall et al., 2011) and in Australia, where old, unproductive soils dominate, the productivity of wetland systems may contrast with surrounding dry habitats more than on other continents. Bat activity around the world increases with nutrient input into wetlands, through nutrient-rich flows (Pereira et al., 2009), pooling and increased terrestrial input through beaver dams (Nummi et al., 2011) or even sewage outflows (Vaughan et al., 1996; Abbott et al., 2009). Floodplain wetlands and river systems, such as in Australia's semi-arid Murray-Darling Basin, can receive large allochthonous inputs from the floodplain, resulting in productivity booms with flooding (Leigh et al., 2010) and high prey production for bats. Large differences in productivity and nutrient availability within wetlands and surrounding areas are also present in urban environments, where stormwater runoff from impervious surfaces (e.g. roads and buildings) may increase nutrient (phosphorus and nitrate) input to wetlands (Birch et al., 2010). Though nutrient rich in-flows can increase bat activity, excessive nutrient input that results in eutrophication may reduce prey diversity (Donohue et al., 2009) and reduce bat activity and foraging (Vaughan et al., 1996). Additionally, wetlands in otherwise unproductive areas may act as refuges for bat species where these areas can serve as a source of reliable prey items (Gonsalves et al., 2013a; Clarke-wood et al., 2016).

Gradients of Salinity

Though bats avoid hypersaline water (Griffiths et al., 2014a), little else is known of their salinity tolerance, or salt loads incurred by foraging on prey from estuarine and saline environments. There is evidence that one fish-eating species, the fish-eating myotis *Myotis vivesi*, can concentrate salt in its urine sufficiently to drink seawater (Carpenter, 1968). Australia has a wide range of estuarine and saline wetland environments (Boon, 2012) where bat activity is high (McKenzie and Rolfe, 1986), including in coastal lagoons (Clarke-wood et al., 2016), mangroves (McConville et al., 2014a), which are also important roost sites (McConville et al., 2013) and saltmarshes, which are productive for mosquito hunting bats (Gonsalves et al., 2013a). Inland arid salt lakes also provide greater sources of invertebrate prey than freshwater lakes of the same region due to increased macrophyte abundance (Kingsford and Porter, 1994). In contrast, anthropogenic-induced salinity can negatively impact wetland biota, potentially affecting bats (Williams, 1999).

Methods

To test our hypotheses we conducted a meta-analysis and review on bats and wetlands in Australia. For this review and meta-analysis, we define "wetland" broadly as any wet habitat including both lotic (e.g. streams) and lentic (e.g. lakes, swamps, floodplains) types. Lotic wetlands were defined as large ($\geqslant$3rd order) streams with water at the time of the study; lentic wetlands were non-stream freshwater inundated areas; intermediate habitats (including estuarine/saline wetlands) were environments which rely on inundation for part of their life cycle but were not inundated at the time of the study; and, dry habitats were all other habitats which were not inundated or subject to periodic inundation.

Meta-analysis of importance of wetlands for bats across ecoregions and environmental gradients

We used acoustic data for our meta-analysis as these were the most readily available and comparable datasets available. However, we still had limited spatial coverage, most notably in the western, central and northeastern parts of the continent (Fig. 1). We took total bat activity data either directly from peer-reviewed publications or from the authors of the publications. All data had been collected during the period from Spring-Autumn, except for Barden (2012) that took place in both wet (November-April) and dry (May-October) seasons of the Northern Territory and Williams and Dickman (2004), collected in winter and spring. Studies that covered large geographic areas (e.g. the Murray-Darling Basin or the wet-dry tropics, Fig. 1) were separated into smaller geographic units or "sites". In total, we used 35 sites from 16 studies, yielding 132 measurements of bat activity. We summarised mean activity with site as the replicate unit, where mean activity was defined as the mean total calls per night (separate calls were call files comprising a sequence of pulses) from acoustic recordings.

For the meta-analysis, we used mean, standard deviation and sample size of bat activity for sites which included measurements of both wetland (either lotic or lentic) and dry habitats, leaving a total of 19 sites from 13 studies and providing 43 comparisons between wet and dry habitats (habitat pairs). We did not use the intermediate habitat type in the meta-analysis due to a lack of data. In one case, we combined two studies in the same location (Sydney, NSW) (Threlfall et al., 2011; Clarke-wood et al., 2016) to form a habitat pair. For most studies, sample size was the number of nights recorded, though in some studies up to two nights were averaged. We quantified the differences between bat activity in wet and dry habitats using the log of the response ratio $L = \ln \frac{X_W}{X_D}$ and associated 95% confidence intervals, where X_W was the mean bat activity at wetland sites and X_D was the mean bat activity at dry sites (Hedges et al., 1999). The value of the log response ratio (L) gave the proportional difference between bat activity in wet and dry habitats, or the effect size. This metric was robust to differences in sensitivity of bat call recorders, as it was a ratio, rather than an absolute value. Where L was greater than zero, bats were more active in wet habitats, where L was less than zero, bats were more active in dry habitats and where L equalled zero, there was no difference in bat activity between wet and dry habitats.

To investigate effects of environmental gradients on effect size, we attributed each site with measures of climate: mean annual temperature (°C), maximum annual temperature (°C), annual rainfall (mm), number of rain days (days >1 mm rainfall) and rainfall variability (percentile analysis method: 90th rainfall percentile minus the 10th rainfall percentile, divided by the 50th percentile) (Bureau of Meteorology, www.bom.gov.au, accessed 2nd February, 2015). All climate measures were based on a 30-year interval (1961–1990), except rainfall variability (1900–2003) (Bureau of Meteorology, www.bom.gov.au, accessed 2nd February, 2015). We also attributed latitude, mean annual net primary productivity (NPP) (gC/m^2 in 10 km resolution) (derived from data from: NASA Earth Observatory 2015) and proportion of woody vegetation cover (within a 10 km radius of each site) (Joint Remote Sensing Research Program 2015) to each site.

To examine wetland importance for bats and the effect of environmental gradients on this importance, we fit ten separate models to the calculated effect sizes, using the restricted maximum-likelihood estimator (REML) method. The first (base) random effects model (no moderator) examined overall effect size across studies and treated differences in effect size across sites as random effects. The remaining models were mixed effects models as they incorporated random variability between sites with fixed effects of explanatory variables (moderators). For the second model we added ecoregion as a fixed moderator to estimate the amount of variability between sites that was attributable to ecoregion. This second model was fitted without an intercept so that estimated coefficients would approximate the overall effect size

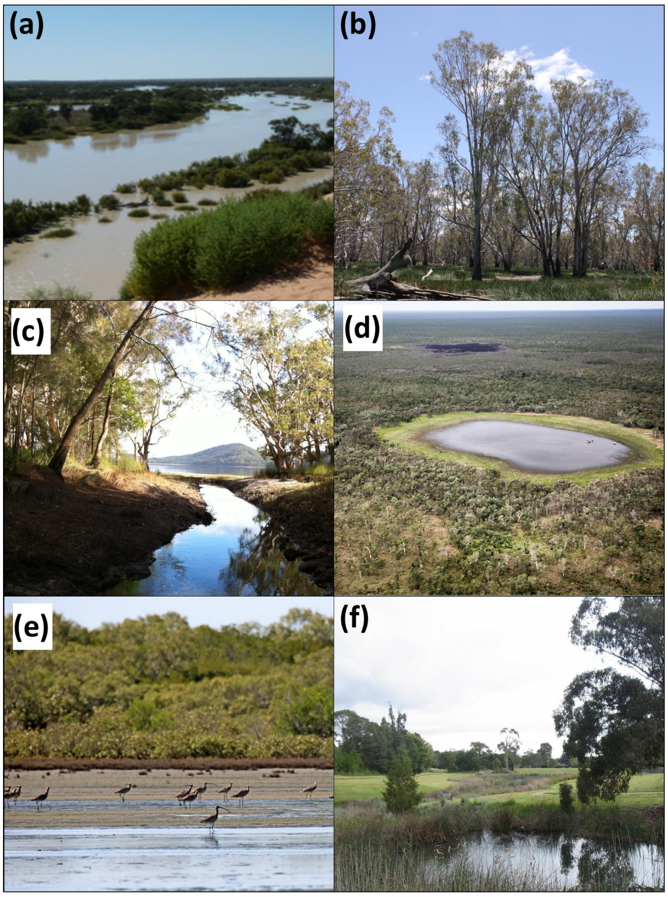

Figure 2 – Wetlands across six ecoregions of Australia: (a) arid (during flood) (Brad Law), (b) semi-arid floodplain, (c) temperate, (d) tropics (Paul Barden), (e) estuarine/saline (Paul Barden) and (f) urban (Tanja Straka). Wetlands include lotic (a,c), lentic (b,d,f) and intermediate (e) types.

for each ecoregion. For the remaining eight models we added each environmental variable separately and one-by-one to the base model as fixed moderators to estimate the amount of variability between sites, attributable to each variable. Variables were added separately because of multiple correlations between variables. Both linear and quadratic fits were tested in case of threshold relationships between effect size and the explanatory variables. To test for the main effect of ecoregion, we compared nested models (one with and one without ecoregion as a moderator) fitted with maximum likelihood, using analysis of variance and the Likelihood Ratio Test (LRT). We used the Wald test to check for significance of the other (continuous) environmental variables. Only variables with a significant relationship with effect size were reported and, where multiple relationships were found for similar explanatory variables (e.g. mean annual temperature and maximum annual temperature), the model with the highest R^2 value was reported. All models were fitted and calculations made using the `metafor` package (Viechtbauer, 2010) in the R statistical environment version 3.1.2 (R Development Core Team, 2014).

Review of literature on bats and wetlands in Australia

We also reviewed the literature on bats and wetlands in Australia, assessing our predictions and results of the meta-analysis. We first searched the peer-reviewed literature using the *Scopus* database for studies about bats and wetlands with three searches: "bat* AND wetland", "bat* AND water" and "bat* AND riparian" in January 2015. We checked each of these references to find Australian studies and also sought unpublished theses and data from trusted sources. We then summarised the literature on the relationships between bats and environmental gradients that affect wetland habitat use for six ecoregions. We chose these ecoregions chiefly based on climate (arid, semi-arid floodplain, temperate, wet-dry tropics), with two separate ecoregions to represent the specific conditions associated with coastal ecosystems (estuarine/saline) and highly developed areas (urban) (Fig. 1 and 2). Finally, we summarised the key threats to bats using wetlands across the six ecoregions.

Results of meta-analysis

Consistent with our predictions, bat activity was significantly higher at wetlands than in dry habitats (Tab. 1, Fig. 3 and 4). Semi-arid, temperate and urban ecoregions had highest mean activity in lotic wetlands while arid and tropics ecoregions had highest mean activity in lentic wetlands (Fig. 4). Only saline/estuarine habitats had highest mean activity in dry areas, though this was not significant (Fig. 4). Effect size differed between ecoregions with about 46% of the variability in effect sizes accounted for by ecoregion (LRT=23.04, p<0.001). In wet climates, including temperate and tropics, bat activity levels were similar between wet and dry habitats, while activity levels between wet and dry habitats differed significantly in dry climates including semi-arid floodplain and arid ecoregions (Tab. 1, Fig. 4). Bats in urban environments generally had greater activity in wet than dry habitats (Fig. 3 and 4), though this was only marginally significant (Tab. 1). Notably, the marginal significance was strongly influenced by two lotic sites. Estuarine/saline habitats showed no evidence for different activity levels between wet and dry habitats (Tab. 1, Fig. 4).

There was a negative linear relationship between annual rainfall and effect size (proportional difference between bat activity in wet compared to dry habitats), suggesting wetland importance for bats increased with aridity (Fig. 5). Wetlands were predicted to become unimportant to bats, when annual rainfall exceeded 1100 mm (Fig. 5). However, there was no evidence for a predicted threshold of aridity, as a linear model fitted the data better than a curvilinear model. Rainfall showed the strongest relationship with effect size (R^2=0.49) but it was difficult to separate the influence of proportion of woody vegetation cover (R^2=0.18) and productivity (R^2=0.15) as these were both correlated with rainfall (R^2>0.79). Our models predicted that wetlands would decrease in importance for bats where mean annual temperatures exceeded 25 °C and latitudes were north of −16° (temperature and latitude were also highly correlated R^2=0.98) (Fig. 5). These relationships were probably influenced by sites in the tropics where there was no relationship between activity and wetlands (Tab. 1, Fig. 4). Woody cover greater than 45% and NPP greater than 1170 gC/m^2 were predicted to diminish importance of wetlands to bats (Fig. 5). Further work is needed to disentangle the interrelated effects of climate, woody cover and productivity on bats. However, these relationships provide preliminary support for the predictions that as moisture decreases, trees become scarce in the landscape and landscape productivity decreases, wetland importance increases for bats.

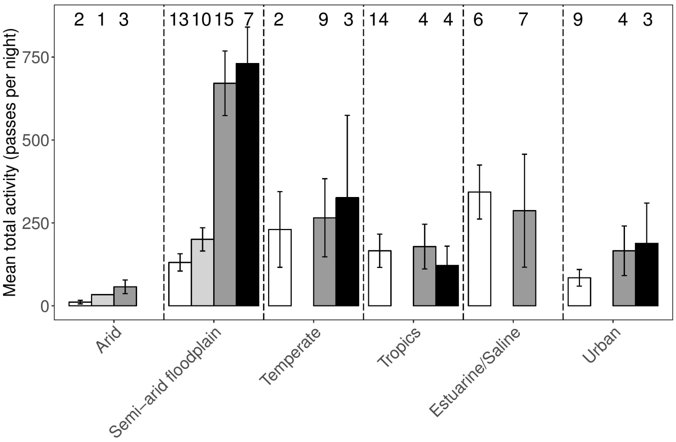

Figure 3 – Mean (±SE) nightly bat activity levels for four habitat types: dry (white), intermediate (pale grey), lentic wetland (dark grey) and lotic wetland (black); across six ecoregions (arid, semi-arid floodplain, temperate, tropics, estuarine/saline and urban) from 16 studies (see Fig. 1 for list). Number of sites is given at the top of the graph for each habitat type in each region.

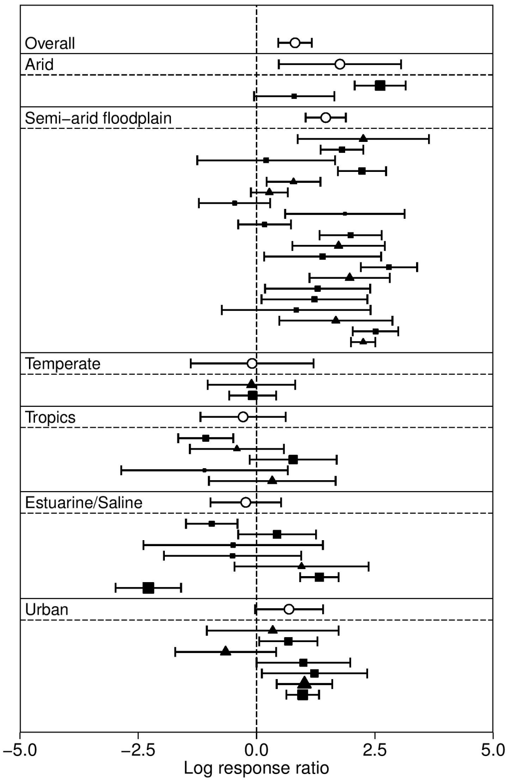

Figure 4 – Quantitative meta-analysis from 13 studies comparing bat activity between wet and dry habitats. Effect sizes for each site (closed symbols) were calculated using the log response ratio ($L = \ln \frac{X_W}{X_D}$), where X_W is the mean bat activity at wetland sites and X_D is the mean bat activity at dry sites (Hedges et al., 1999). Comparisons between both lotic and dry sites (closed triangles) and lentic and dry sites (closed squares) are shown. Error bars are 95% confidence intervals and size of points is proportional to natural log of the sample size (n ranged from 3–96). Positive values indicate greater activity within wetlands while negative values indicate greater activity in dry habitats. Overall effects across regions and for each region separately (open circles) were calculated by fitting models using the restricted maximum-likelihood estimator (REML) method.

Review of Ecoregions

Arid

Two recent global reviews of the use of water resources by bats noted that arid regions are understudied (Korine et al., 2016; Salvarina, 2016). This holds true in Australia, where little is known about the ecology of bats in the vast arid zone of Australia or specifically how they respond to the dramatic swings in resource condition, driven by irregular cycles of dry and flood periods. Deserts have low productivity resulting in low diversity, with even the tropical deserts of Western Australia supporting only 7–9 bat species (McKenzie et al., 2002). Fast-flying species dominate, foraging in open spaces and over large spatial scales. Most bats need to drink water regularly, especially during reproduction (Adams and Hayes, 2008), though urine-concentrating abilities of some desert bats (Happold and Happold, 1988) and torpor, can reduce water loss (Bondarenco et al., 2013). These adaptations are likely to contribute to persistence of some species, far from water sources. In the Simpson and Great Sandy Deserts, with contiguous arid areas of over 176500 km^2, bats concentrated around permanent or temporary water, rather than in dry open habitats (Coles, 1993; Williams and Dickman, 2004). In our meta-analysis, bat activity was higher in wet compared to dry habitats, though this was based on only two studies that compared wet and dry habitats in arid regions (Tab. 1, Fig. 3 and 4).

What happens to bat activity when arid conditions change and the once empty wetlands and rivers are inundated? The occurrence of significant rainfall associated with La Niña events in both 2010 and 2011 provided an opportunity to investigate how bats responded to large flooding events in arid areas. In 2011, bats were sampled along the Warburton River (Kalamurina Sanctuary) upstream of Kati Thanda in central Australia, soon after peak flooding and while extensive surrounding areas remained inundated with water (B. Law and M. Lean *unpubl. data*). Acoustic detectors recorded bat activity over three consecutive nights at a mixed set of river, dune and swale sites, all within 3 km of the Warburton River. There were nine sites: four claypan wetlands/swales, two dune crests and three sites along the Warburton River. As surface water was widespread during the survey, Law and Lean (*unpubl. data*) predicted that bat activity would be spread across the inundated areas, contrasting with dry periods when bat activity was more likely to be concentrated near the channel of the Warburton River. Just 458 calls were recorded from nine sites, sampled for a total of 270 hours. Diversity was moderate with six bat taxa (a species grouping that could not be identified to species level *Scotorepens greyii*/*M. eleryi* contributed the most activity - 34% of all calls). There was little difference in bat activity between dune crests and swale/claypan sites, but it was three times higher over open water of the flooding river, indicating the considerable importance of this river channel even during a wet climatic phase. These patterns are comparable to open habitats and areas of permanent water in the Simpson Desert (Williams and Dickman, 2004), where riverine habitats have higher productivity than the surrounding ephemeral floodplain (Free et al., 2013). The low overall activity and diversity of bats at arid sites likely reflects a combination of low productivity (McKenzie et al., 2002) and a scarcity of roosts, especially tree hollows. Australian bats typically breed once a year, producing one or two young (Churchill, 2009), providing less opportunity to rapidly respond to flooding events by increasing populations through reproduction shown by birds and small mammals (Letnic et al., 2005; Kingsford et al., 2010).

In arid landscapes artificial watering points (AWPs) may be more common than natural ones, providing an important resource for bats (Korine et al., 2016). One of the few studies of bats at AWPs in Australia was by Velez (2001), who identified high bat activity and richness at AWPs relative to water-remote areas on the stony downs of Sturt National Park, NSW. Velez (2001) concluded that arid zone bats depend

Table 1 – Summary of one random effects (model 1, base model) and six mixed effects (models 2–7) models that modelled the heterogeneity in effect sizes for 19 sites in Australia comparing wet to dry habitats. For model 2, no intercept was included, so modelled estimates approximate average effect sizes estimated in each ecoregion. The test statistic used to calculate z and p values was the Wald statistic. Modelled relationships are shown graphically with 95% confidence intervals in Fig. 4 (models 1–2) and Fig. 5 (models 3–7). Only statistically significant relationships were included in Tab. 1 and Fig. 4 and 5.

Model no.	Explanatory variables	Estimate	SE	z value	p value
1	-	0.812	0.182	4.474	<0.001
2	Ecoregion (arid)	1.761	0.659	2.674	0.008
	Ecoregion (semi-arid floodplain)	1.461	0.217	6.726	<0.001
	Ecoregion (temperate)	−0.094	0.662	−0.142	0.887
	Ecoregion (tropics)	−0.285	0.460	−0.620	0.535
	Ecoregion (estuarine)	−0.228	0.380	−0.600	0.548
	Ecoregion (urban)	0.685	0.367	1.864	0.062
3	Intercept	2.169	0.273	7.949	<0.001
	Annual rainfall (mm)	−0.002	<0.001	−5.685	<0.001
4	Intercept	3.466	0.885	3.918	<0.001
	Mean annual temperature (°C)	−0.136	0.044	−3.049	0.002
5	Intercept	1.379	0.252	5.465	<0.001
	Proportion woody cover within a 10 km radius	−2.778	0.933	−2.977	0.003
6	Intercept	−0.973	0.626	−1.555	0.120
	Latitude (degrees)	−0.062	0.021	−2.970	0.003
7	Intercept	1.459	0.293	4.976	<0.0001
	Mean annual productivity (gC/m^2)	−0.001	<0.001	−2.718	0.007

on AWPs not only for foraging, but also for drinking, given females may require water during reproduction (Adams and Hayes, 2008). However, AWPs negatively impact ecosystems due to the concentrated grazing pressure from native and introduced herbivores (James et al., 1999) and as a result, their closure has been recommended as an important management action to benefit biodiversity. AWPs are more likely to be functionally equivalent to wetlands for bats if they are large enough to allow a range of species to drink (Hall et al., 2016) free of obstructions over surface water (Tuttle et al., 2006) and contain riparian vegetation (Straka et al., 2016a). Further work is needed to quantify the importance of AWPs for bats in arid Australia, especially during lactating season. Watering points for bats may once have been widespread, given prevalence of Aboriginal dug wells and dams in arid areas (Gammage, 2011) as well as wetlands supplied by the groundwater from the Great Artesian Basin, such as mound springs (Fensham and Fairfax, 2003).

Bats closely associate with wetlands and riparian zones in arid Australia, even during climatic wet phases, but the relative importance of tree roost availability, productivity or availability of surface water for drinking remains unknown. Our meta-analysis provides some preliminary evidence that landscape scarcity of trees and low productivity in the landscape may increase wetland importance for bats (Fig. 5).

Semi-arid floodplain

Australia is the flattest continent in the world with large areas of inland floodplain. Some of the most significant floodplains occur within the Murray-Darling Basin in the southeast of Australia. This basin contains diverse water-dependent ecological communities while supporting 39% of the country's agricultural production (MDBA, 2010). The Murray-Darling Basin covers a wide range of climates with alpine sourced rivers in the south east and highly ephemeral semi-arid systems in the north-west. While the arid regions of Australia are also influenced by highly variable flooding, we deal with the semi-arid floodplain separately, given its distinct bat ecology. Semi-arid floodplains generally have at least one permanent or semi-permanent water source, usually a high order stream, producing distinct bat assemblages between arid and semi-arid areas (Lumsden and Bennett, 1995; Monamy et al., 2013). Variable flooding regularity leads to a mosaic of wetland habitat types, including permanently flooded, regularly flooded (every 1–2 years) and occasionally flooded (every 5–10 years), to which bats respond differently (Blakey et al., 2017). Finally, the semi-arid floodplain is distinct from many arid floodplains as its water is often extensively regulated for human use (Kingsford, 2000) reducing populations of aquatic depdendent organisms more than unregulated basins (Kingsford et al., 2017) and likely affecting bats.

Compared to surrounding dry and agricultural areas, floodplain habitats are disproportionately important for bats in the semi-arid zone (Blakey et al., 2017). Where open water is present (rivers and lakes) bats are 5 times more active and forage 14 times more than in dry vegetation (Blakey et al., 2017). Flooding regimes in semi-arid wetlands also influence forest structure, driving how bats use these floodplain wetlands. Open savanna woodlands dominate the wooded areas of the Murray-Darling Basin, with patches of dense regrowth forest, and dieback of mature trees (Cunningham et al., 2009) from altered hydrological conditions (Bren, 1992). Bat activity can decline in these dense regrowth stands by up to 22 times, compared to surrounding open habitats (Blakey et al., 2016). Further work to separate foraging activity from drinking activity (Griffiths, 2013) and long-term studies are needed to understand the dynamic relationships between bats, their prey and flooding dynamics.

The difference between activity of bats in wetlands and dry areas is greater for the semi-arid floodplain than for all other ecoregions (Fig. 3). Supporting this, capture rates for bats were much greater at water than away from it in semi-arid Victoria and Queensland (Lumsden and Bennett, 1995; Young and Ford, 2000). In semi-arid landscapes with a network of perennial streams, mesic and arid species coexist, creating a large species pool that can be comparable to temperate mesic habitats (Young and Ford, 2000). Additionally, almost all areas surrounding remaining floodplain wetlands and riparian areas have been cleared for agriculture in temperate regions. Consequently, many roosting (and for some species, foraging) opportunities are confined to the floodplain forest, woodland and riparian zones (Lumsden et al., 2002). This contrast in roosting opportunities is magnified as hollows are abundant in trees associated with riparian and floodplain zones (e.g. black box *Eucalyptus largiflorens* and river red gum *E. camaldulensis*) (Bennett et al., 1994). Similarly, in more arid areas (corresponding to north-western parts of the floodplain towards central

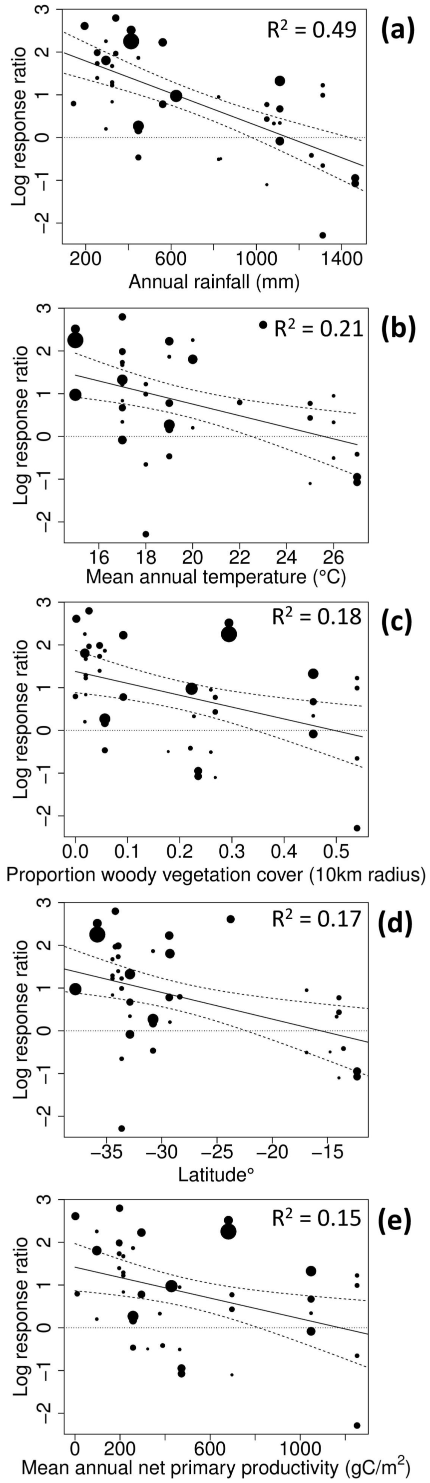

Figure 5 – The relationship between effect size comparing bat activity between wetlands and dry habitats (log response ratio) and (a) annual rainfall, (b) mean annual temperature, (c) proportion of woody vegetation cover (within a 10 km radius of sites), (d) site latitude, and (e) mean annual net primary productivity (NPP). Modelled relationships are shown (solid line) with 95% confidence intervals (dashed line) (see Tab. 1 for model details). Sizes of points are proportional to the inverse standard error for each effect size. Positive effect sizes (y axes) indicate greater activity within wet than dry habitats while negative values indicate the opposite.

Australia), the largest and often the only trees with abundant hollows grow in floodplains and along rivers.

In a study across >400000 km^2 of the Murray-Darling Basin, Blakey et al. (2017) found that nine out of 14 taxa positively associated with floodplain habitats compared to dry vegetation. These included Australia's only trawling bat, *M. macropus*, which is reliant on open surface water for foraging and roosting (Robson, 1984; Campbell, 2009, 2011) as well as three mesic species that are predominantly coastal in distribution: large forest bat *V. darlingtoni*, southern forest bat *V. regulus* and chocolate wattled bat *Chalinolobus morio* (Lumsden and Bennett, 1995; Law and Anderson, 1999; Monamy et al., 2013). Even Molossid species were positively associated with floodplain habitats within the Murray-Darling (Blakey et al., 2017) despite this family being well adapted for arid environments. Specifically, Ride's free-tailed bat *Mormopterus ridei*, appears to select wet habitats within semi-arid floodplains along the River Murray (Reside and Lumsden, 2011).

Temperate

Warm-cool temperate ("temperate") areas of south-eastern and south-western Australia support extensive eucalypt forests with a variety of tree species. Tall wet sclerophyll forest with dense mesic understories, more open dry sclerophyll forest or grassy open woodland can dominate depending on rainfall, topography and soil. Contrasting with bat activity in arid and semi-arid floodplain, there was little evidence from the meta-analysis of any differences in bat activity between wet and dry habitats in temperate regions (Tab. 1, Fig. 4). Since some studies have reported very high activity levels in temperate wet habitats, especially over lotic wetlands (e.g. 822 call night^{-1}, Law and Chidel, 2002), we should interpret these results cautiously given low sample sizes and prioritise future work comparing wet and dry temperate environments.

Our review also indicated open spaces over streams provided important habitat for bats in temperate forests where there was high productivity for foraging, linear habitat with low clutter and freshwater for drinking (Law and Chidel, 2002; Lloyd et al., 2006). However, temperate streams are likely to have comparatively low productivity, generally an order of magnitude lower than tropical streams (Davies et al., 2008). It has been hypothesised that *M. macropus* has low activity in temperate forest streams, due to low productivity compared to lower reaches (Anderson et al., 2006; Lloyd et al., 2006), though quantification of insect resources near water in temperate areas is needed to confirm this. The low productivity hypothesis is consistent with selective clearing of vegetation for agriculture on the more productive soils of Australia, leaving less productive forested areas (Pressey, 1994). Remnant woodland of agricultural landscapes support high activity levels of bats in south-eastern Australia (e.g. Lumsden and Bennett, 2005; Lentini et al., 2012), but neither bats nor nocturnal insects responded to the proximity of water (Lentini et al., 2012), potentially because surface water was extensive from recent rainfall at the time of survey.

In general, bat activity is low in the temperate riparian zones of small headwater streams, probably because of high clutter levels (Law and Chidel, 2002; Cawthen et al., 2012). As stream size increases, species' richness and activity for a range of species also increases (Lloyd et al., 2006; Law et al., 2011), suggesting that increasing gaps and open space areas over large streams (but also in other features such as tracks and trails) contribute to maintaining diverse assemblages. Two open-space adapted molossids were the species most strongly associated with flyway size in mountainous sclerophyll forest (Lloyd et al., 2006). Linear open spaces are likely to be most important in dense cluttered forest, such as forest regenerating after disturbances like logging or wildfire (Law and Chidel, 2002; Lloyd et al., 2006). In the dry woodlands of the temperate region, bat activity levels can be extremely high over water (Law et al., 1998)(Law et al. 1998).

Temperate coastal areas also support lentic wetlands, significant for bats. Floodplains and extensive freshwater wetlands provided high quality habitat for threatened species, such as the east-coast freetail bat Mormopterus norfolkensis, an open-space adapted bat (McConville et al., 2014a). Wetlands and riparian vegetation along streams also provide habitat for roosting bats in temperate regions, with many species roosting near water (Tidemann and Flavel, 1987; Lunney et al., 1988; Law and Anderson, 1999; Law and Chidel, 2004; Webala et al., 2010). For example, *M. macropus* consistently roosts near water, often beneath bridges spanning streams (Campbell, 2009) or in mangroves (McConville et al., 2013).

Tropics

The tropics extend across the far north of Australia (Fig. 1), comprising the wet tropics and the wet-dry tropics. The wet tropics are a small 440 km stretch of coastline and adjacent ranges extending from Cooktown to Townsville, in Queensland. They are characterised by very high seasonal rainfall (1200 to 4000 mm year^{-1}, IUCN, 1988), relatively high topographic relief and a lack of landscape burning, with rainforest communities dominant (Fig. 1). The wet-dry tropics extend across the remainder of the region (Fig. 1) and are characterised by moderate to high seasonal rainfall (500 to 1800 mm year^{-1}), relatively low topographic relief, frequent landscape burning, with eucalypt woodlands dominant. The wet tropics wetlands cover about 1169 ha (DEHP, 2014) while the wet-dry tropics region contains 51 river catchments and an estimated 6.5 million ha of wetlands (Lukacs and Finlayson, 2010). Wetlands are a major contributor to riparian food webs in the tropics. For example, insect biomass in Kakadu National Park was greatest over streams and at the water's edge than in riparian and savanna areas (10–15 m and 160 m from the stream bank, respectively), mainly because of large numbers of adult aquatic insects (Lynch et al., 2002).

We found no evidence that bat activity levels differed between wet and dry habitats within the tropics in our meta-analysis (Tab. 1 and Fig. 3). Four out of five studies in the tropics showed no difference in bat activity between wet and dry habitats and one study showed greater activity in dry habitats (Fig. 4). We predicted a weaker response to wetland habitats by bats within the tropics, as compared to other eco-regions, due to the overall high moisture levels, greater availability of wetlands and riparian areas in the landscape and high productivity. However, we predicted higher activity over wet compared to dry habitats, due to the availability of aquatic prey.

In the tropical savannas of far northern Australia, bat species richness increased with decreasing distance to perennial rivers (Milne et al., 2005). But riverine sites supported similar species assemblages to woodland sites, even during the driest time of the year. Vegetation corridors near rivers and surrounding areas, rather than the water, were considered the important environments for high bat species richness (Milne et al., 2005), which is at odds with the pattern of insect distribution (Lynch et al., 2002). Vegetation of riparian environments usually has a distinct "outer edge" bordering short and relatively open dry vegetation, allowing a diversity of environments for bats with different foraging strategies (Milne et al., 2005).

In the rainforests of the wet tropics of north-eastern Australia, lotic rather than lentic wetlands are the dominant "wet" habitat. The importance of riparian areas has not been investigated, but we predict that the linear open stretches above larger and wider streams in otherwise dense forest would support a rich assemblage of bat species, similar to temperate environments. Similar to the wet-dry tropics, the high moisture levels throughout the landscape may reduce the dependency of bats on riparian zones of tropical rainforest.

Several bat species in the tropics are associated with wet habitats, including the Arnhem sheath-tailed bat *Taphozous kapalgensis* and the northern pipistrelle *Pipistrellus westralis* that use lowland floodplains, mangroves and swamps (Milne and Pavey, 2011). The pygmy long-eared bat *Nyctophilus walkeri* occurs along creeks and rivers within escarpment areas (Milne et al., 2006; Milne and Pavey, 2011), while the northern coastal free-tailed bat *Mormopterus cobourgianus* occurs in mangroves (Armstrong, 2011). The relationship between wetlands and bats in the tropics clearly warrants further research, especially considering the extensive wetlands throughout the tropics (e.g. Kakadu National Park) where there is both high richness of bats and significant conservation value (Milne et al., 2006).

Saline/estuarine

Saline and estuarine wetlands provide key roosting and foraging habitat for many species but bats did not use them significantly more than surrounding dry habitats in our meta-analysis (Tab. 11, Fig. 3 and 4). Saline or estuarine areas, such as saltmarsh, mangroves and brackish lagoons, are extensive in the tropics. Tropical mangroves support rich bat communities, with diverse foraging strategies (McKenzie and Rolfe, 1986). In temperate regions, old stands of mangroves (e.g. grey mangrove *Avicennia marina*) support hollows and stable microclimate for maternity roosts for a suite of bat species, including open-space species such as the threatened *M. norfolkensis* (McConville and Law, 2013; McConville et al., 2013). Also in temperate Australia, coastal saltmarsh, classified as an "endangered ecological community", provides open and productive bat foraging habitat, especially for mosquitoes (Gonsalves et al., 2013a). For example, near Newcastle NSW, prey abundance was high in saltmarsh and nearby forest and while bat activity was greatest in forest habitat, proportional feeding activity was greatest in saltmarsh (Gonsalves et al., 2013a). Furthermore, prey abundance was positively correlated with total bat activity only in open saltmarsh, where prey availability to bats was likely to be higher, due to the increased detectability in the uncluttered habitat (Gonsalves et al., 2013a). This pattern was strongest for small, high frequency (>50 kHz) echolocating vespertilionids (*Vespadelus* spp.) as these small bats caught abundant mosquitoes while large bats did not (Gonsalves et al., 2013b). These vespertilionids also shifted their home ranges according to shifting fluctuations of mosquito abundance in the coastal landscape (Gonsalves et al., 2013c). In brackish lagoons, high bat activity occurs over expanses of open water (Clarke-wood et al., 2016), providing important habitat for trawling *M. macropus* (Clarke-wood et al., 2016).

Urban

As at 2013, 89% of Australia's population lived within urban areas (The World Bank, 2013). Urban sprawl completely transforms or destroys natural areas (McKinney, 2008; Werner and Zahner, 2009) and insectivorous bats are among the relatively few native mammal fauna that persist in Australian urban areas (van der Ree and McCarthy, 2005). In our meta-analysis, four out of seven urban comparisons showed greater bat activity in wet habitats (Fig. 4), reflected in overall means (Fig. 3), though this trend was only marginally significant (Tab. 1). Our results were strongly influenced by a study of suburban bushland fragments, where dry habitats were compared to lotic sites just 2–10 m wide (data from Threlfall et al., 2011). Omitting these data, urban ecoregions had significantly higher activity over wetlands (z=2.3, p=0.023) than dry habitats, with a mean effect size of 0.89. In sandstone gullies in Sydney, small streams were not used extensively by bats (Basham et al., 2010), probably due to the generally lower fertility of sandstone areas (Threlfall et al., 2011), smaller size and clutter. Additionally, positive effects of wetlands may be confounded by different levels of woody vegetation cover and urbanisation, given these factors are associated with bats and their prey in urban areas (Basham et al., 2010; Wilson, 2013). When tree cover and degree of urbanisation (road density within a buffer of 1 km) were held constant between wet and dry habitat comparisons in Melbourne (Straka et al., 2016a), there was a strongly positive association between bats and wetlands. The urban wetlands available to this study were also all from the temperate zone, so many of the previously discussed factors influencing bat wetland use in the temperate zone are likely to influence these urban bats.

Overall, availability of drinking water, potential roost trees and abundant insect prey are likely drivers of the importance of wetlands within the urban matrix (Straka *unpubl. data*). In a study of bats in urban wetlands in Melbourne, nightly bat activity was 2.5 times higher at wetlands compared to ecologically similar dry sites (Straka et al., 2016a)). Furthermore, each urban wetland supported on average 10% more bat species than ecologically similar dry areas (Straka et al., 2016a). As expected, water was an important predictor for most bat species, including a small bat species *V. vulturnus* (Straka et al., 2016a), probably due to their preference to feed on small aquatic emergent insects such as dipterans. The importance of these insects for *V. vulturnus* likely explains this species shifting its foraging range in association with the abundance of mosquitoes (Gonsalves et al., 2013c). More tree hollows (83.7±26.3 hollows ha^{-1}) and more nocturnal flying insects captured in light traps (249±49) also occurred in urban wetlands, compared to ecologically similar urban sites without water (3.2±2.2 hollows ha^{-1}; 160±30 insects). Trichopterans and dipterans were 4–5 times more abundant at wetlands when water was present than in similar dry sites (Straka *unpubl. data*).

Riparian vegetation surrounding wetlands play an important role for urban bats. In Melbourne, the southeast of Australia, wetlands with trees fringing the wetland margins had greatest bat richness, with 10.4 species compared to just 5.9 species where no trees were present in Melbourne (Straka et al., 2016a). Furthermore, riparian areas here had significantly higher insect abundance and biomass compared to residential areas, remnant bushlands, industrial areas, parks, and golf courses (Wilson, 2013). Higher bat activity also occurred in riparian areas and bushland in Sydney, compared to open space or backyard sites (Threlfall et al., 2011). Riparian areas may be critical for movement between resource patches within the urban mosaic for clutter-adapted species, for example the eastern horseshoe bat *Rhinolophus megaphyllus* (Hourigan et al., 2006). Overall, the evidence suggests that wetlands, including brackish lagoons, within the extensively modified urban matrix act as highly productive bat habitat (Clarke-wood et al., 2016; Straka et al., 2016a). Interestingly conservation and management efforts in riparian vegetation might not only benefit bats and insects, but also people. As a study in Melbourne showed, nearby residents of urban wetlands had high preferences for wetlands with a high vegetation complexity (more trees, understorey and emergent aquatic vegetation) which were also found to support a higher number of bat species and several orders of prey insects (Straka et al., 2016b).

Review of threats to bat communities of australian wetlands

Globally, 87% of wetlands have been lost since the 18th century (Davidson, 2014). In Australia, wetlands continue to be lost at a rate of 1.066% per year (Kingsford et al., 2016). The deterioration of wetland ecological character relevant to bats is driven by threats such as clearing of vegetation, modification of natural flow regimes, urban expansion and water pollution (Jones et al., 2009). All of these threats are likely to be exacerbated by the continued impacts of anthropogenic climate change (Jenkins et al., 2011).

Clearing of Vegetation (Terrestrial, Riparian and Aquatic)

Clearing of terrestrial, riparian and aquatic vegetation is a major threat to Australian wetlands and the bat communities they support. The loss of wetlands in southern Australia has been implicated in the decline of one of Australia's most endangered bat species, the southern bent-winged bat *Miniopterus orianae bassanii*, by reducing its preferred foraging habitat (Lumsden and Jemison, 2015). Additionally, tree removal reduces availability of suitable roosts, especially for species that prefer to roost in floodplains (Lumsden et al., 2002; Campbell, 2009). Removal of vegetation in Western Australia has increased salinity of rivers and wetlands (20 times greater than natural), negatively affecting biota (Halse et al., 2003). Such impacts on bats are unknown but prey availability is likely to be reduced. Loss of native vegetation may also occur through exotic weed invasion, affecting bats in the tropics and arid zones (Milne and Pavey, 2011). Dominance of exotic pasture grasses increases fuel loads, leading to frequent intense fires that may kill bat roost trees (Milne and Pavey, 2011), while woody shrubs are replacing large areas of floodplain wetlands in the tropics (Braithwaite et al., 1989).

Removal of vegetation surrounding wetlands changes the flow of subsidies to terrestrial ecosystems (Greenwood, 2014). For example, reducing surrounding vegetation decreases productivity of aquatic ecosystems by reducing the allochthonous input of leaves and shifting food webs to more algal-driven than detritus-driven (Robertson et al., 1999); this can decrease supply of emergent insect prey to bats (Nakano and

Murakami, 2001). Wetlands and riparian vegetation can decrease eutrophication through uptake of nutrients from runoff (e.g. agricultural activities), with removal of vegetation decreasing water quality at a catchment scale (Verhoeven et al., 2006) affecting bat habitat quality (Langton et al., 2010; Clarke-wood et al., 2016). Conversely, the reduction of shading, caused by vegetation clearing, may also increase prey abundance by increasing periphyton growth (Towns, 1981). Vegetation loss can also affect bats at the landscape scale through fragmentation of wetland networks, important for foraging and migratory movements (Flaquer et al., 2006; Lookingbill et al., 2010). Also, fragmentation at the landscape level affects abundance and composition of prey (Hunter and Hunter, 2002). Loss of native vegetation affects all Australian ecoregions but particularly those most strongly impacted by agricultural (semi-arid floodplain and temperate regions), and urban expansion (urban and estuarine/saline regions).

Modification of Natural Flow Regimes: River Regulation

The rivers of Australia's Murray-Darling Basin, comprising the semi-arid floodplain region, are highly regulated, containing 248 large dams with a storage capacity of 125% mean annual runoff with 66% being diverted for irrigation (Finlayson et al., 2013). These alterations have dramatic effects on basin ecology, demonstrated by long-term negative trends in wetland biota in regulated, as compared to unregulated basins (Kingsford et al., 2017). Ecological effects of river regulation include: large-scale canopy dieback (Cunningham et al., 2009) and loss of breeding habitat for fish (Gehrke et al., 1995), birds (Kingsford and Thomas, 1995) and frogs (Wassens and Maher, 2011), though effects on bats are still largely understudied (Blakey, 2017).

River regulation reduces the areal extent of wetlands (Kingsford and Thomas, 1995, 2002), reducing foraging, roosting and drinking habitat for bats (Blakey, 2017). Additionally, changes to seasonal timing of flows can influence floodplain productivity (Robertson et al., 2001) and prey. Differences in prey abundance and access to water may be especially important during the breeding season for lactating bats when energetic and water-balance demands are acute (Kurta et al., 1989; Adams and Hayes, 2008). Indeed, bat activity and prey availability decrease dramatically with lowered river flow in arid systems (Hagen and Sabo, 2012, 2014), as does bat reproductive output (Adams, 2010). Declines in flooding due to river regulation have caused widespread dieback of floodplain forests, up to 70% in some parts of the Murray-Darling (Cunningham et al., 2009). While bats also use stags (snags) as roosts, this level of dieback can alter the long-term availability of roosts within the floodplain. Reduced flows have also led to acidification of wetlands in South Australia where acid sulphate soils occur (Kingsford et al., 2011), affecting invertebrate communities and potentially bats. River regulation is particularly damaging to bats in the semi-arid floodplain, which is most impacted by Australia's dams and water regulatory structures, though water regulation also affects river and floodplain systems in the temperate and tropics ecoregions (Kingsford, 2000).

Urban expansion

Urban bats experience a combination of all of threats dealt with here, and occupancy of the majority of south eastern urban-dwelling bat species has been reported to drop dramatically with increasing housing density (Caryl et al., 2016). Threats that are particular to urban expansion include urban runoff and light pollution. Urban runoff can lead to an accumulation of heavy metals in wetland sediment (Walsh et al., 2001; Pettigrove and Hoffmann, 2003), which has been linked to decreasing species richness of bats in Melbourne wetlands (Straka et al., 2016a). Importantly, heavy metal pollution and artificial light was negatively associated with the activity of Australia's only trawling bat, *M. macropus* in Melbourne (Straka et al., 2016a). Wetlands in Melbourne with high levels of artificial nocturnal light had lower bat activity and bat species richness compared to areas with lower levels of artificial light (Straka et al., 2016a). Artificial nocturnal light is particularly detrimental for slow-flying clutter adapted species such as Gould's long-eared bat *Nyctophilus gouldi*, which may be more susceptible to predation than fast-flying species (Threlfall et al., 2013). Most Australians live along the coast where continued urban expansion will pressure estuarine and saline wetlands, and further affect bat foraging and roosting habitats (McConville et al., 2013; Gonsalves et al., 2013a).

Pollution

Pollution of aquatic ecosystems by industry, agriculture, urban expansion or mining can contaminate bat food webs with heavy metals, agricultural pesticides (allinson et al., 2006) and residues from mining dams (e.g. cyanide) (Griffiths et al., 2014b). Contaminants can accumulate in bat tissue (Naidoo et al., 2013), potentially affecting their immune system (Lilley et al., 2013), or juvenile survivorship (Frick et al., 2007). Exposure to contaminants is expected to be higher for bats foraging over wetlands, as aquatic emergent prey directly interact with contaminants, sometimes accumulating them (e.g. chironomids) without affecting survival of these prey (Krantzberg and Stokes, 1989). Reflecting this, a study in Mexico found that specialist fish-eating bats had higher metal concentrations compared to a species that consumed both fish and terrestrial prey (Méndez and Alvarez-Castañeda, 2000). Metal inputs into wetlands, such as lead, copper, or high concentrations of zinc may reduce prey diversity (Pettigrove and Hoffmann, 2005) and ultimately bat activity and foraging (Straka et al., 2016a).

Many pesticides, like persistent organochlorines, are still recorded in bat tissues of Australian bats (allinson et al., 2006), despite their ban in the 1970s and 1980s (Bayat et al., 2014). Lactating bats such as Mexican free-tailed bats can transfer up to 82% of dichlorodipehnyl dichloroethylene (DDE) loads to their young (Clark et al., 1975). Organochlorines, and other emerging organic contaminants like polybrominated diphenyl ethers (PBDEs), polybrominated biphenyls (PBBs) and pentachlorophenol (PCP), can have lethal, acute and chronic sub-lethal effects on bats (Bayat et al., 2014). Other contaminants like polycyclic aromatic hydrocarbons (PAHs) are discharged into the environment through incomplete combustion processes from industrial, domestic and natural sources (Preuss et al., 2003). The most volatile member of this family of contaminants is Naphthalene, occurring at double its concentration between larval and adult stages of chironomids in contaminated areas (Reinhold et al., 1999), potentially affecting pond bats *Myotis dasycneme* which forage on chironomids (Reinhold et al., 1999). Australian bats that forage over water or on small dipterans, such as *M. macropus* and *Vespadelus* spp., may be similarly at risk.

Pollution also simplifies food webs, decreasing diversity of available prey (Hogsden and Harding, 2014), while increasing the abundance of some pollution-tolerant prey groups (Abbott et al., 2009). This affects bat species differently, for example nutrient-enrichment (e.g. Nitrate and Phosphorus from agricultural and urban runoff) can increase foraging opportunities for some species but reduce prey for others (Kalcounis-Rueppell et al., 2007; Abbott et al., 2009). In a global review of bats use of aquatic habitats, Salvarina (2016) found that of 11 bat species, two responded negatively to declines in water quality, one responded positively and the remaining species showed either no response or variable responses (e.g. both positive and negative) to decreases in water quality. In coastal lagoons of NSW, *M. macropus* was absent from the most degraded coastal lagoons (Clarke-wood et al., 2016). Pollution of wetlands is likely affect bats in all ecoregions, given their mobility and attraction to water to drink and forage.

Climate Change

Climate change threatens bats in all ecoregions (Jones et al., 2009; Sherwin et al., 2013) as with other Australian wetland fauna and flora (Jenkins et al., 2011; Finlayson et al., 2013). Consistent with global trends (Hughes, 2003), temperature rises of several degrees are predicted in Australia by 2070, along with increased frequency of extremely high temperature days (Pearce et al., 2007). Bats with small distributions or specialised niche requirements may be particularly affected by high temperatures as they may not be able to shift their range (Sherwin et al., 2013). More intense tropical cyclones are predicted along with sea level rises (Pearce et al., 2007) potentially impacting near-coastal freshwater wetlands through salt-water intrusion (Jenkins et al., 2011) and destruction of low-lying mangrove forests. For example the extensive coastal floodplain of Kakadu in the tropics are only 3–4 m above sea level and saltwater intrusions in the past has caused large areas of paperbark swamp to be replaced by saline mudflats (Finlayson et al., 2009).

Reduced rainfall is also predicted for the southern part of the continent, accompanied by more frequent and severe droughts leading to decreases in surface water of the semi-arid floodplain of about 11% by 2030 (Leblanc et al., 2012). Coupled with pressures of river regulation, these climate effects could irreversibly affect semi-arid floodplain wetlands, like the Macquarie Marshes in NSW, where wetland ecology depends on frequent and variable flows (Jenkins et al., 2011). These ecological changes may shift the type, amount and timing of prey for bats, affecting reproductive output of bat populations, which has already been observed in arid North America (Adams, 2010). Climate change is also projected to increase climate variability in regions affected by ENSO (south-eastern Australia, including the semi-arid floodplain) (Meehl et al., 2000); intensifying boom and bust cycles. Increased drying and variability of water in arid and semi-arid areas could potentially reduce the geographic ranges and populations of bats that rely on water sources.

Conclusion

We identified several important patterns in bat use of wetland habitats on the Australian continent and found support for all three of our predictions. At the continental scale, bats were more active over wetlands than surrounding dry habitats. As predicted, wetland importance increased with increasing aridity, likely reflecting the increased importance of wetlands where drinking water, productive foraging habitat and roosting structures are scarce. Supporting this, bats were similarly active in wet and dry habitats within temperate and tropical regions, likely due to the high moisture and water availability in the landscape. We did not find support for an aridity threshold, after which the difference in activity between wet and dry habitats would decrease, though this pattern may be revealed by further targeted studies.

As predicted, there were strong positive associations between wetlands and bat activity within highly modified areas. This included the semi-arid floodplain (which has been extensively cleared for agriculture), and four out of seven sites in the highly modified urban ecoregion. Additionally, as trees became increasingly rare and as landscape productivity decreased, wetland importance increased for bats. However, these relationships were difficult to disentangle from negative relationships with other, correlated covariates (e.g. annual rainfall, mean annual temperature and latitude). Importantly, semi-arid floodplain and urban ecoregion wetlands, and associated bat communities, also face the strongest threats including: vegetation clearing, modification of flow regimes, urban expansion, pollution and climate change.

Our study is an overview of the importance of wetlands to bats in Australia and further research is urgently needed. Firstly, our findings should be tested using paired sampling with particular care given to controlling for the effects of different types of wet habitats and contextual environmental variables, such as tree cover. These studies should especially target the large areas where we were missing data in the northeastern, western and central parts of the continent. Furthermore, more species-level research is required into how bats use wetlands for foraging, roosting and moving in the landscape. One species in particular, *M. macropus*, depends on wet habitats for all its life cycle and inhabits all but arid ecoregions. This may be a useful focal species for future monitoring of threats to Australian wetlands. Finally, information on how threats to wetlands affect bat habitat availability, prey communities, reproduction, physiology and survival has barely been studied and is sorely needed.

Despite the obvious knowledge gaps, it is clear from our study that wetlands are important for bats and that these wetlands and their bat communities face numerous threats. Preserving wetlands for Australian bat communities will require a much greater commitment by federal and state governments in: establishing protected area networks, science-informed management (e.g. strategic adaptive management), threat reduction including protection and restoration of wetland condition (including flow regimes) and reducing carbon emissions (Kingsford et al., 2016).

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