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

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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 macroinvertebrates (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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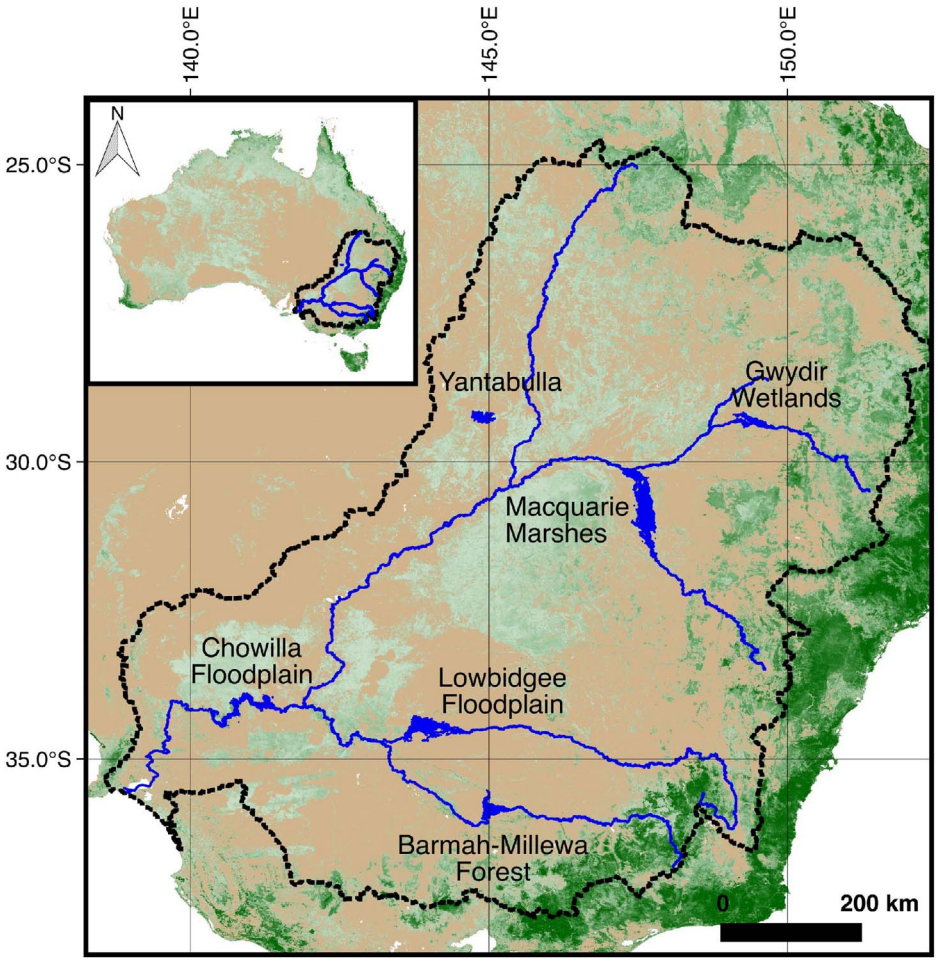

Fig. 1. Bats and insects were sampled at six floodplain systems within of the Murray-Darling Basin (black dashed line) in south-eastern Australia. Floodplain extent of the six floodplain systems and main rivers are shown in blue and degree of green shading reflects increasing canopy cover around the 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