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Threatened but not conserved: flying-fox roosting and foraging habitat in Australia

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Abstract. Conservation relies upon a primary understanding of changes in a species' population size, distribution, and habitat use. Bats represent about one in five mammal species in the world, but understanding for most species is poor. For flying-foxes, specifically the 66 *Pteropus* species globally, 31 are classified as threatened (Vulnerable, Endangered, Critically Endangered) on the IUCN Red List. Flying-foxes typically aggregate in colonies of thousands to hundreds of thousands of individuals at their roost sites, dispersing at sunset to forage on floral resources (pollen, nectar, and fruit) in nearby environments. However, understanding of flying-fox roosting habitat preferences is poor, hindering conservation efforts in many countries. In this study, we used a database of 654 known roost sites of the four flying-fox species that occur across mainland Australia to determine the land-use categories and vegetation types in which roost sites were found. In addition, we determined the land-use categories and vegetation types found within the surrounding 25 km radius of each roost, representing primary foraging habitat. Surprisingly, for the four species most roosts occurred in urban areas (42–59%, $n = 4$ species) followed by agricultural areas (21–31%). Critically, for the two nationally listed species, only 5.2% of grey-headed and 13.9% of spectacled flying-fox roosts occurred in habitat within protected areas. Roosts have previously been reported to predominantly occur in rainforest, mangrove, wetland, and dry sclerophyll vegetation types. However, we found that only 20–35% of roosts for each of the four species occurred in these habitats. This study shows that flying-fox roosts overwhelmingly occurred within human-modified landscapes across eastern Australia, and that conservation reserves inadequately protect essential habitat of roosting and foraging flying-foxes.

Keywords: bat, fruit-bat, pollinator, conservation, threatened species, Pteropus, vegetation community, mammal.

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Introduction

Globally, more than 8500 vertebrate species are threatened with extinction (IUCN 2020). Habitat destruction and degradation, as a result of human land use, are largely considered the driving threats to biodiversity (Chaudhary and Mooers 2018; Powers and Jetz 2019). As such, habitat protection is frequently prioritised in species conservation planning (Possingham *et al*. 2002; Wintle *et al*. 2019). However, habitat protection is not always sufficient to ensure species persistence, and a multitude of approaches are often necessary for the successful conservation of threatened species (Hayward 2011). Understanding species habitat requirements and use remains crucial for developing effective conservation action plans.

Flying-foxes (*Pteropus* spp.) roost colonially, typically in groups of thousands to hundreds of thousands of individuals, and often in habitat containing relatively large, emergent trees, close to floral resources for nocturnal foraging (Granek 2002; Gulraiz *et al*. 2015; Oleksy *et al*. 2015). Of the 66 *Pteropus* species globally, six are extinct and 31 are considered at risk (Vulnerable, Endangered, or Critically Endangered) on the IUCN Red List (Todd 2019). Four species of flying-fox are native to the Australian mainland: grey-headed (*Pteropus poliocephalus*), spectacled (*P. conspicillatus*), black (*P. alecto*), and little red (*P. scapulatus*) flying-fox. The grey-headed flying-fox is recognised both nationally and internationally as Vulnerable to extinction (TSSC 2001; IUCN 2020), and the spectacled flying-fox is nationally Endangered in Australia (TSSC 2019). Globally, a lack of understanding regarding flying-fox roosting behaviour and habitat requirements hinders population assessments and conservation planning.

Historically, Australian flying-fox roosts have predominantly been described as associated with natural habitats including mangroves, wetlands, rainforests and, to a lesser extent, dry sclerophyll eucalypt (Palmer and Woinarski 1999; Fox 2011; McClelland *et al*. 2011). In recent years, however, colonies have increasingly become associated with urban landscapes (Williams *et al*. 2006; Plowright *et al*. 2011; Tait *et al*. 2014). Several urban 'benefits' have been proposed. These include night-time lighting improving navigation, altered climatic suitability of urban areas, and a mixture of native and exotic plants providing more reliable nectar and fruit resources year-round (Vardon and Tidemann 1999; McDonald-Madden *et al*. 2005). However, the exact causes for an increased use of urban areas by flying-foxes are yet to be determined, as little is known about the roosting and foraging habitat preferences of flying-foxes in urban environments.

Flying-fox roosts located close to urban areas are commonly criticised by the public for being loud and odorous, and posing a disease risk (Edson *et al*. 2015; Currey *et al*. 2018). Conflict can lead to ineffective and potentially damaging management strategies such as roost dispersal (Roberts *et al*. 2011; Lentini and Welbergen 2019). Conflict may also occur in agricultural areas, with flying-fox foraging damaging crops (Divljan *et al*. 2011). These conflicts are exacerbated by patterns of roost occupancy that appear to be driven by local foraging resources (Giles *et al*. 2016; Vanderduys *et al*. 2020). At times, local flowering can lead to large temporary influxes of flying-foxes, which can lead to or exacerbate conflict (Lentini and Welbergen 2019). An extreme example of this has been observed in response to mast flowering of spotted gum (*Corymbia maculata*) where ~250 000 grey-headed flying-foxes moved to the Water Gardens roost located in Bateman's Bay, New South Wales, where the community responded with intense calls for dispersal of this vulnerable species (Welbergen and Eby 2016). At present, it is unknown on what basis flying-foxes choose their roost sites, which renders management agencies unable to design 'carrot solutions' that help reduce conflict by creating more attractive roost sites elsewhere. Understanding the local distribution of roosts, and how they are selected by the four mainland Australian flying-fox species can therefore be highly informative for both the management and conservation of these species and to inform land managers where human–wildlife conflicts occur.

Flying-foxes provide the ecosystem services of pollination and seed dispersal to their forage plants (Law 1995; Palmer *et al*. 2000; Markus and Hall 2004; Parsons *et al*. 2006; Eby and Law 2008; Hahn *et al*. 2014). Because of the scale of their movements, flying-foxes are of particular importance in fragmented landscapes (Welbergen *et al*. 2020). It could be argued that flying-foxes are ecologically more important in an anthropogenic landscape, as their foraging behaviour connects fragmented vegetation (see Westcott *et al*. 2015; Welbergen *et al*. 2020). Studies assessing flying-foxes' foraging behaviour report that nightly movements predominantly occur within a 25 km area surrounding roosts (Roberts 2012; Welbergen unpub. data) and landscape scale movements of up to 300 km in a night (Welbergen *et al*. 2020).

For the four mainland Australian flying-fox species, we described the location and species composition of known diurnal roosts supporting colonies. We then assessed the land classification of each roost: protected, urban, or agricultural. We also assessed the vegetation classification associated with each roost. Lastly, we assessed the land classification and vegetation type within the surrounding 25 km of each roost.

Methods

The four mainland Australian flying-fox species are distributed across tropical regions in the north to the warm-temperate regions of eastern Australia (Fig. 1) (Parish *et al*. 2012). Grey-headed flying-foxes have the southernmost distribution of any flying-fox species, spanning from Queensland around to South Australia (Westcott *et al*. 2011). The black flying-fox is a predominantly tropical species, ranging the northern coastline of Australia, and over the past two decades has spread south from Queensland along the east coast of New South Wales (Welbergen *et al*. 2008; Roberts *et al*. 2012) with vagrant records in Victoria. Little red flying-foxes have the most extensive distribution, spanning from Western Australia across the north of Australia to Queensland and south to Victoria. Spectacled flying-foxes have the most restricted distribution of the four species, being found in the wet tropics and Cape York in north Queensland in Australia (Garnett *et al*. 1999; Fox 2011).

Flying-fox colonial roost data

The National Flying-fox Monitoring Program (NFFMP) (Westcott *et al*. 2011) has produced a spatial dataset of the location of known roosts for the four mainland species of flying-fox across Australia, with a focus on grey-headed and spectacled flying-fox colonies. As part of the NFFMP, all known roosts were surveyed quarterly for flying-foxes between November 2012 and February 2017 (n = 18 surveys). Roosts were added during the survey period; these could be newly occupied by flying-foxes or have previously been occupied but were unknown. A concerted effort was made to identify and survey all roost locations, this was aided by concurrent telemetry studies of all species during the initial years of the NFFMP (Westcott *et al*. 2015; Welbergen *et al*. 2020). A total of 654 roosts were surveyed across Australia during the period covered by this study and all roosts where flying-foxes were observed are included. NFFMP coverage of parts of north Queensland, the Northern Territory, and Western Australia was incomplete due to remoteness and accessibility and as a consequence there were insufficient data for these areas.

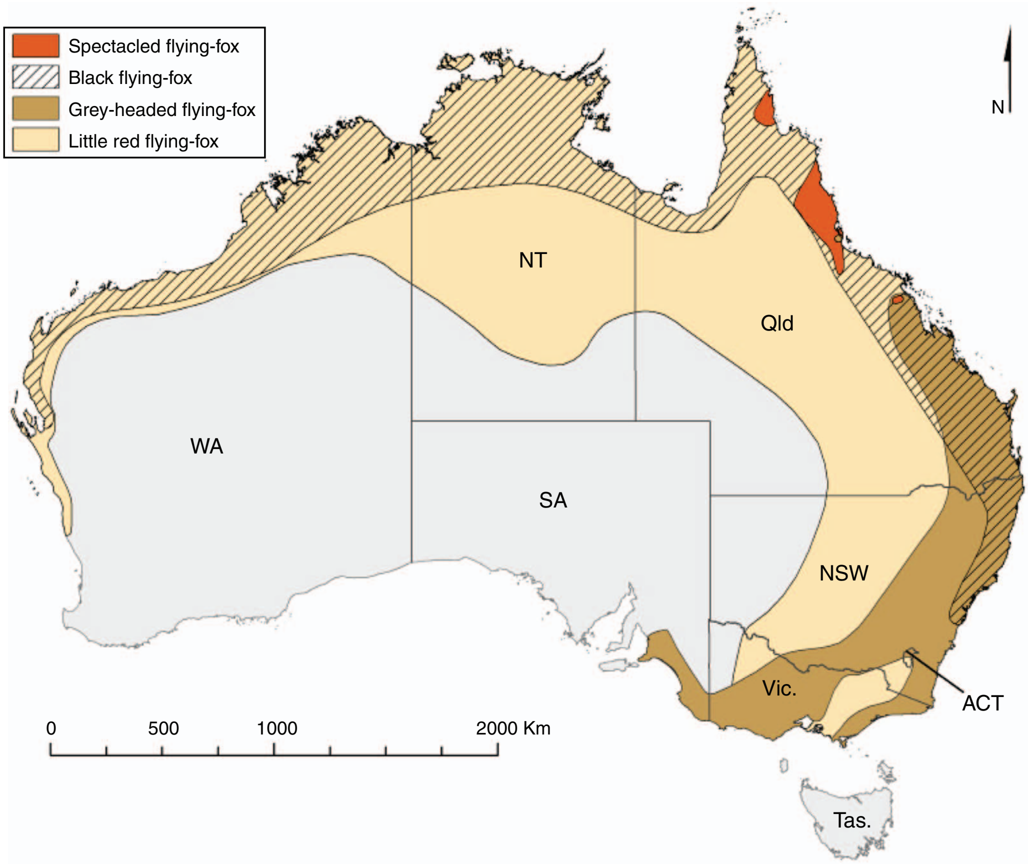

Fig. 1. Distribution of the four mainland Australian flying-fox species. Map by Pia Lentini 2018.

We initially classified each roost as 'active' or 'inactive' based on the 18 NFFMP surveys recording the presence of at least one flying-fox species within the sampling period; only active roosts were included in analyses (n = 430) (Table 1). Surveys were conducted at all locations known to have had colonial roosting over recent decades, and thus some roosts were not used by flying-foxes at all within the sampling period. Data from active roosts were then categorised into single- and mixed-species colonies across the sampling period. This resulted in three datasets for each species: (1) all locations where a species occurred (total active roosts); (2) all locations where only a single species was recorded (single-species roosts); and (3) all locations where two or more species were recorded (mixed-species roosts).

Table 1. Number of active, mixed- and single-species flying-fox roosts identified during 18 quarterly surveys, 2012–2017

Species	Total active roosts	Mixed-species roosts	Single-species roosts
All roosts	430	266 (61.7%)	164 (38.3%)
Grey-headed flying-fox	310	232 (74.8%)	78 (25.2%)
Black flying-fox	291	247 (84.6%)	44 (15.4%)
Little red flying-fox	156	141 (90.4%)	15 (9.6%)
Spectacled flying-fox	36	9 (25%)	27 (75%)

Spatial data

To identify the land use categories that coincided with the location of active flying-fox roosts across Australia, we developed a land use map by combining data from Land Use of Australia 2010–11 and the Collaborative Australian Protected Areas Database (CAPAD) 2014 (Supplementary Material, Table S1). Where conflicting land use categories occurred, we used the land use classification from the more recent CAPAD. The Land Use of Australia dataset contained 18 categories. We combined these into seven broad categories: protected areas; minimal use; grazing and native vegetation; forestry; agriculture; urban; and mining and waste. This dataset was used to identify the number of active roosts located within each of these land use categories. We manually inspected all data points that returned no data or water values at the roost location (n = 17); using satellite imagery, as well as proximate data to inform our decisions, we assigned a land use category to these locations.

Roost land use and vegetation

We used the National Vegetation Information System (NVIS) data with Present Major Vegetation Groups (DEWR 2007), to assess the primary vegetation types in which flying-fox roosts were located nationally (Supplementary Material, Table S1). We used this dataset to determine vegetation type at the roost location (point), as well as the proportion of vegetation types within the surrounding 25 km area (buffer; see below). The NVIS data contained 33 categories; however, only 18 categories were identified in association with roost locations, and thus other categories were not reported for simplicity. As flying-fox roosts sometimes occur in aquatic habitat (e.g. mangroves, wetland) or riparian vegetation, we manually inspected all data points assigned as 'water' at the roost location. Using satellite imagery and proximate data to inform our decisions, we assigned a vegetation type to these locations, as well as any location returning 'no data' (n = 28).

Foraging (buffer) land use and vegetation

We assessed the land use category and vegetation composition within the 25 km area (primary foraging habitat; 'buffer') surrounding roosts, representing flying-foxes' nocturnal foraging range (Roberts 2012; Welbergen, unpub. data). Of the 33 vegetation types present within the 25 km buffer region surrounding each roost, three vegetation categories ('mallee woodland and shrublands', 'other open woodlands', and 'other grasslands, herblands, shrublands') were not recorded within buffers and were therefore excluded from further analyses. All other categories were recorded within buffers. We added an oceanic water category to our land use category dataset, using World Water Bodies data (Supplementary Material, Table S1), to accurately differentiate between the proportion of buffers for coastal roosts for which there were no data, and what was simply ocean. 'Water' and 'no data' values were retained for buffer calculations.

Analysis

Spatial datasets (Supplementary Material, Table S1) were imported into ArcGIS 10.4, using standard tools to change projections to Geocentric Datum of Australia 1994 where necessary. We extracted values of all variables for each active roost location for the four species at two spatial scales: at the roost (point) and within a 25 km radius (buffer). A 25 km radius was chosen to reflect the main foraging zone around a colony, which corresponds to nocturnal tracking surveys of these species (Roberts 2012; Welbergen, unpub. data).

To identify how the location of colonies was related to land use and vegetation type, we intercepted colony location with land use and NVIS data. We calculated the percentage of the 25 km buffer made up by each land use and vegetation category for each colony using 'Tabulate Intersection' tools in ArcGIS. Descriptive statistics were calculated using standard tools in R software (R Core Team 2017).

Results

Of the 654 roost sites in our dataset, grey-headed flying-foxes were recorded at 310 roosts, black flying-foxes at 291 roosts, little red flying-foxes at 156 roosts, and spectacled flying-foxes at 36 roosts (Tables 1, 2). In total, 430 active roosts were identified over the 5-year period (2012–2017) through the NFFMP. Of these, 61.7% were mixed-species roosts (Table 1). The most common species compositions at mixed-species roosts were grey-headed and black flying-foxes (n = 124), followed by grey-headed, black, and little red flying-foxes (n = 94) (Table 3).

Table 2. Jurisdictions in which flying-fox roosts were identified during 18 quarterly surveys, 2012–2017

Note: no data were available for Western Australia

Species	Qld	NSW	Vic.	SA	NT	ACT
All roosts	256	153	15	1	4	1
Grey-headed flying-fox	152	141	15	1	0	1
Black flying-fox	205	83	0	0	3	0
Little red flying-fox	110	40	3	0	3	0
Spectacled flying-fox	36	0	0	0	0	0

Table 3. Mixed-species composition and number of flying-fox roosts identified during 18 quarterly surveys, 2012–2017

Species composition	No. of roosts
Two species	
Grey-headed and black	124
Grey-headed and little red	12
Grey-headed and spectacled	1
Black and little red	27
Black and spectacled	0
Little red and spectacled	6
Three species	
Grey-headed, black and little red	94
Grey-headed, little red and spectacled	0
Black, little red and spectacled	1
Four species	
Grey-headed, black, little red and spectacled	1

Land use associated with roosts

The more common land use categories associated with all species of flying-fox roosts were urban (55.1%) and agricultural (23.5%) land (Table 4). Protected land accounted for only 6.7% of roost locations. Land use of the remaining roosts was classified as: 'minimal use' (6%), 'mining and waste' (0.2%), 'forestry' (1.2%), and 'grazing, native vegetation' (7.2%) (Table 4). At the species level, few roosts were in protected areas: grey-headed (5.2%), black (6.2%), little red (3.8%) and spectacled flying-fox (13.9%) (Table 4). For the four species, most roosts were classified as urban land use: grey-headed (58.7%), black (59.1%), little red (54.5%), and spectacled flying-fox (41.7%) (Table 4).

The land use classification within the 25 km radius surrounding flying-fox roosts was diverse, but predominantly comprised agricultural (24.6%), urban (14.4%), and protected (14%) land (Table 5). Agricultural land was the most common land use category within the buffers around grey-headed (25.2%), black (23.1%), and little red (32.9%) flying-fox roosts. However, protected land was the most common land use category within the buffers around spectacled flying-fox roosts (36%) (Table 5). Urban areas represented a smaller proportion of buffers for each species: grey-headed (17.5%),

Table 4. Land use categories of flying-fox roosts assessed during 18 quarterly surveys, 2012–2017
Note: more than one species can be recorded at a roost (see Table 3)

Land use category	All roosts (n = 430)	Grey-headed flying-fox (n = 310)	Black flying-fox (n = 291)	Little red flying-fox (n = 156)	Spectacled flying-fox (n = 36)
Protected	29 (6.7%)	16 (5.2%)	18 (6.2%)	6 (3.8%)	5 (13.9%)
Urban	237 (55.1%)	182 (58.7%)	172 (59.1%)	85 (54.5%)	15 (41.7%)
Agricultural	101 (23.5%)	70 (22.6%)	61 (21%)	43 (27.6%)	11 (30.6%)
Minimal use	26 (6%)	19 (6.1%)	13 (4.5%)	9 (5.8%)	2 (5.5%)
Grazing and native vegetation	31 (7.2%)	18 (5.8%)	24 (8.2%)	13 (8.3%	3 (8.3%)
Forestry	5 (1.2%)	5 (1.6%)	2 (0.7%)	0	0
Mining and waste	1 (0.2%)	0	1 (0.3%)	0	0

Table 5. Land use category within the 25 km foraging habitat (buffer) around flying-fox roosts identified during 18 quarterly surveys, 2012–2017

Land use category	All roosts (n = 430) Mean ± s.d.	Grey-headed flying-fox (n = 310) Mean ± s.d.	Black flying-fox (n = 291) Mean ± s.d.	Little red flying-fox (n = 156) Mean ± s.d.	Spectacled flying-fox (n = 36) Mean ± s.d.
Protected	14.02 ± 11.93	12.66 ± 9.10	11.29 ± 8.31	10.26 ± 9.67	35.96 ± 14.70
Urban	14.43 ± 17.08	17.15 ± 18.28	16.62 ± 17.34	11.60 ± 15.36	2.90 ± 2.47
Agricultural	24.57 ± 22.15	25.19 ± 21.57	23.13 ± 20.18	32.90 ± 26.45	13.34 ± 9.33
Minimal use	6.80 ± 3.80	7.10 ± 3.85	7.31 ± 3.63	6.45 ± 3.85	5.82 ± 3.23
Grazing and native vegetation	13.70 ± 12.15	12.70 ± 8.94	14.56 ± 11.55	17.94 ± 15.07	8.78 ± 11.56
Forestry	4.46 ± 6.94	4.64 ± 7.24	3.88 ± 6.70	4.52 ± 7.54	5.96 ± 4.99
Mining and waste	0.14 ± 0.34	0.16 ± 0.38	0.15 ± 0.32	0.14 ± 0.45	0.01 ± 0.02
Water (inland)	1.02 ± 1.43	1.09 ± 1.55	0.88 ± 1.17	0.88 ± 1.31	0.85 ± 0.78
Water (oceanic)	20.17 ± 20.32	18.65 ± 19.42	21.39 ± 20.90	14.79 ± 19.64	25.74 ± 18.95
No data	0.69 ± 0.79	0.66 ± 0.80	0.80 ± 0.87	0.52 ± 0.74	0.64 ± 0.40

black (16.6%), little red (11.6%), and spectacled flying-fox (2.9%) (Table 5).

Vegetation associated with roosts

The most common vegetation class associated with flying-fox roosts was 'cleared, non-native vegetation, buildings' (59.8%) (Supplementary Material, Table S2), which we confirmed largely corresponded to urban and agricultural land. This vegetation class was the most common for all species: grey-headed (57.4%), black (64.3%), little red (66.7%), and spectacled flying-fox (58.3%) (Supplementary Material, Table S2). Relatively few roosts were in the vegetation categories typically reported in the literature (Supplementary Material, Table S2), such as 'rainforest and vine thickets' (8.4%), 'melaleuca forests and woodlands' (5.3%), 'mangroves' (5.1%), and eucalypt-dominated categories (17.3%; includes: 'eucalypt open forest' 8.1%, 'eucalypt woodlands' 6.7%, 'eucalypt tall open forest' 2.1%, 'eucalypt low open forest' 0.2%, 'tropical eucalyptus woodlands/ grasslands' 0.2%).

The most common vegetation class associated with the 25 km foraging range (buffer) surrounding flying-fox roosts was 'cleared, non-native vegetation, buildings' (43.7%) (Supplementary Material, Table S3). 'Cleared, non-native vegetation, buildings' also represented the largest proportion of the 25 km buffer areas for grey-headed (47.1%), black (46.5%), and little red (48%) flying-fox roosts. However, 'rainforests and vine thickets' represented the largest proportion of buffers for spectacled flying-fox roosts (27.2%) (Supplementary Material, Table S3). Native vegetation categories accounted for the next largest proportion of buffer areas for all roosts: combined 'eucalypt' dominated categories (23.8%), 'rainforest and vine thickets' (5.0%), 'melaleuca forest and woodlands' (1.0%), 'mangroves' (0.8%) (Supplementary Material, Table S3).

Discussion

This study highlights a serious lack of protection of roosting and foraging habitat for all four Australian mainland flying-fox species. Given the major role that roost sites play in the life of flying-foxes, protecting roosting and foraging habitat is considered a central component of flying-fox conservation and management. In contrast, however, only 13.9% of the roosts of the Endangered spectacled flying-fox and 5.2% of the Vulnerable grey-headed flying-fox were in protected areas. This also applied to the two non-listed species, with only 3.8% of little red and 6.2% of black flying-fox roosts in protected areas. Likewise, within the 25 km foraging range surrounding roosts of grey-headed, black, and little red flying-foxes, only 15% of land use was classified as protected areas. However, protected land was the largest category surrounding spectacled flying-fox roosts (36%). The lack of habitat protection and relative importance of anthropogenic landscapes for the four species highlights the need to consider the human dimensions of human–wildlife conflict for sound management and conservation of Australia's flying-foxes (Kung *et al*. 2015; Currey *et al*. 2018).

More than half of grey-headed, black, and little red flying-fox roosts and over a third of spectacled flying-fox roosts were located in land uses categorised as urban. Since the 1800s many Australians have viewed flying-foxes as unwelcome in agricultural areas (Ratcliffe 1938). Over recent decades, human–wildlife conflict in urban areas has increased, with some colonies dispersed by human intervention (Ruffell *et al*. 2009; Roberts *et al*. 2011; Currey *et al*. 2018). Such dispersals have rarely been successful, given our poor understanding of the factors driving roost use (see Welbergen *et al*. 2020) and establishment. This study showed that, across eastern Australia, flying-fox roosts occurred overwhelmingly in human-modified landscapes and not in protected areas. As a consequence, a conservation approach that primarily focuses on protected areas can only poorly protect flying-fox roosts. Given that our data suggested Australian flying-fox species predominantly roost in urban areas, and other data that indicate this may be increasing (Tait *et al*. 2014), conservation strategies need to be multifaceted, addressing roost habitat protection outside formally protected areas along with public perception and education.

Of the 430 roosts assessed in this study, most were in human-modified vegetation, categorised as 'cleared, non-native vegetation, buildings', and were located across eastern Australia. This finding dramatically revises our understanding of the preferred roosting vegetation used by flying-foxes in Australia. After modified habitats, roosts were predominantly in rainforests, woodlands, and mangroves, which align more closely with the established vegetation selected for flying-fox roosts (Palmer and Woinarski 1999; Fox 2011; McClelland *et al*. 2011). These native vegetation communities were again prominent within the 25 km buffer surrounding roosts and contain the plant species most likely to benefit from the landscape scale ecosystem services (pollination and seed dispersal) provided by flying-foxes (Eby and Law 2008).

The data presented cover the known distribution for the grey-headed flying-fox (Parish *et al*. 2012) but inadequately incorporated distributions of the black and little red flying-fox; both species also occur across northern and north-western Australia, which were poorly sampled, and are likely to support a larger number of roosts in natural areas. Furthermore, our current understanding fails to consider the wider distribution of the spectacled flying-fox, into Papua New Guinea, and the black flying-fox into Papua New Guinea and Indonesia. Critically, there are also limited data available on how the location of roosts and flying-fox species assemblages have changed over recent decades. The distribution of flying-fox species is highly variable, exemplified by shifts in black and grey-headed flying-foxes in recent years (Roberts *et al*. 2012). To improve conservation planning, and community education, further information on the dynamics of occupancy of roosts (Meade *et al*. 2019; Welbergen *et al*. 2020) and how these are related to changes in the surrounding landscape (Giles *et al*. 2016) would be informative. In addition, an evaluation of flying-foxes' ecosystem services (pollination and seed dispersal), relevant to maintaining healthy forests (see Fujita and Tuttle 1991), could benefit initatives to enhance conservation efforts.

Unsurprisingly, given the overlapping distributions of the flying-fox species, roost locations predominantly supported multiple species, with relatively few observations of single-species roosts. The NFFMP focussed on the two listed species but complementary observations of black and little red flying-foxes across their distribution were documented; further research is needed. The NFFMP and telemetry studies (Westcott *et al*. 2015; Welbergen *et al*. 2020) identified many previously unknown roosts. Discovering and monitoring these roosts should improve flying-fox population estimates (Westcott *et al*. 2011, 2015), and further enhance our understanding of the roost habitat preferences of the species. It must be noted that the data presented and the effort to identify roosts was extensive, yet it is inevitable that some roosts remain unidentified and new roosts form and are not detected in response to the availability of local food resources. An increasingly concerning threat to flying-foxes are mass die-offs associated with extreme temperature events exacerbated by climate change (Welbergen *et al*. 2008, 2014). Combining land use and vegetation data at known roost locations with weather forecasts could further improve predictions of the likelihood and severity of heat stress events on flying-fox colonies (Ratnayake *et al*. 2019) by accounting for the thermal buffering properties of land use categories and vegetation types. Increasing our understanding of the factors driving flying-fox habitat selection, and how these vary seasonally and annually, are integral to the recovery and long-term conservation of flying-foxes in Australia.

Conclusion

We demonstrated that, in eastern Australia, flying-foxes were predominantly using human-modified landscapes to roost and forage. This finding demonstrates flying-foxes' adaptability, and suggests that in Australia this group of species may be more resilient to habitat change than species that are entirely dependent upon undisturbed habitat. The reasons for flying-foxes' adaptation to modified landscapes are poorly understood, yet it creates key challenges for flying-fox management and conservation. This highlights the need for better understanding of the drivers of flying-fox urbanisation and the consideration of human dimensions in the management and conservation of these iconic species. Flying-foxes provide unique landscape-scale pollen and seed dispersal services, particularly connecting Australia's increasingly fragmented forest ecosystems, thus enhanced protection of the ecological services they provide should be a conservation priority. Critically, conservation of the two listed species in Australia, the spectacled and grey-headed flying-foxes, is poorly represented by protected areas, and roosts and individuals are exposed to human–wildlife conflict in the human-modified landscapes where the species increasingly occur (Williams *et al*. 2006; Plowright *et al*. 2011; Tait *et al*. 2014). Future research should assess what drives flying-foxes to shift towards anthropogenic areas, as knowledge of such drivers will be key for informing policy and practice to better manage and conserve these species, especially in human-modified landscapes. Lastly, future research should assess flying-fox colony size and breeding with respect to land use to inform roost conservation planning.

Conflicts of interest

Justin Welbergen is a guest Associate Editor. Despite this relationship, he did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor of this journal. The authors have no further conflicts of interest to declare.

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