



# OPEN The Bat Ripple case study shows ecological and economic contributions of grey headed flying foxes in Australia

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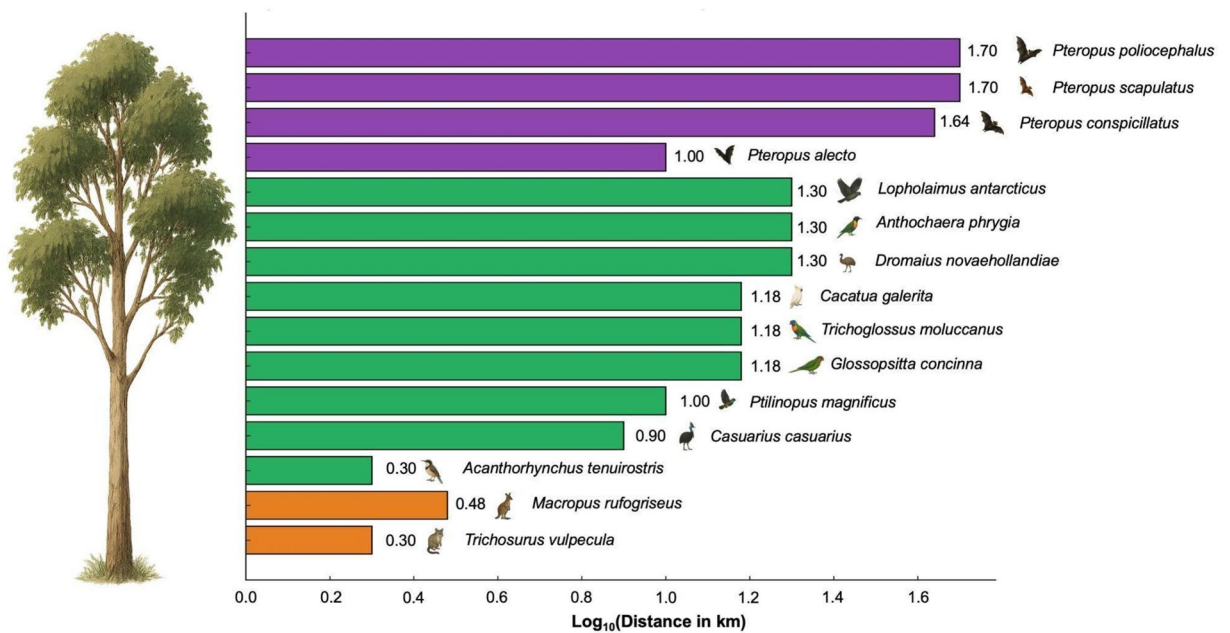
Old World fruit bats (Pteropodidae) are globally important pollinators and seed dispersers. While their ecological services have been valued in parts of West Africa and Southeast Asia, no such estimates exist for Australia. Here, we introduce the Bat Ripple, quantifying the spatial extent and potential ecological and economic impact of flying foxes across continental Australia. Using data from the CSIRO National Flying-Fox Monitoring Program (2012–2022) and species-specific foraging distances (3–50 km), we first map the potential foraging influence of 1209 roosts of the four mainland flying fox species, estimating that these bats influence 11.6–41.4 million hectares, including forests, plantations, and restoration areas. We then focus on a scenario-based valuation using 465 selected grey-headed flying fox (*Pteropus poliocephalus*) roosts, which alone are estimated to facilitate a median of ~91.6 million new trees annually across their maximum foraging range. We show that pollination services could potentially contribute between AUD \$ 271 million and 955 million per year to the eucalypt timber industry. Our findings highlight the potential role of flying foxes in sustaining both ecosystem function and economic productivity in Australia.

Old World fruit bats have long been recognized as one of Earth's most critical keystone species providing fruit dispersal and pollination services across four continents and 65 countries sustaining ecosystems that support millions of people<sup>1–3</sup>. The foremost reason for this is their ability to move long distances, up to 500 km in 48 hours<sup>4</sup>. Coupled with high densities and their foraging at high canopy levels, flying foxes occupy an almost exclusive niche in most regions as long-distance agents of seed and pollen dispersal across vast landscapes<sup>5–7</sup>. Previous studies have attached economic valuations to these flying fox dispersal and pollination services including estimation of forest regeneration potential in West Africa<sup>8</sup>, and pollination and fruit production valuations in peninsular Malaysia<sup>9</sup>. However, no such attempt has been made in an Australian context, where the third largest population of fruit bats occurs, and where rates of land-use change and deforestation are among the highest in the world<sup>10,11</sup>. This question is all the more relevant in the context of recent climate change fueled heating events, which have caused significant declines in flying fox populations, with at least 34 documented heat stress events affecting roosts across eastern Australia since 1994<sup>12,13</sup>.

In this paper we introduce what we term a Bat Ripple to describe the spatial extent and potential ecosystem services provided by Australia's grey-headed flying fox *Pteropus poliocephalus*, black-headed flying fox *Pteropus alecto*, little red flying fox *Pteropus scapulatus*, and spectacled flying fox *Pteropus conspicillatus* across their continental range. We first map the Bat Ripple by estimating the potential foraging influence of all four species across Australia. We then develop a scenario-based ecological and economic valuation focused on *P. poliocephalus*, extending this Bat Ripple across critical Australian habitat conservation and production areas. This approach provides the first systematic attempt to quantify the ecosystem service value of Australian flying foxes and highlights the potential consequent impact bat loss could have on forest succession dynamics, pollination, and dispersal across the timber industry, and even unforeseen carbon sequestration (Fig. 1).

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**Fig. 1.** Maximum nightly (nocturnal) or daily (diurnal) foraging distances of Australia's four flying fox species (*Pteropus* spp.) compared to other frugivores and pollinators, highlighting their influence for seed rain and pollination services. Mean urban and non-urban buffers used for ecosystem service calculations are: grey-headed flying fox (6.78 km urban, 11.935 km non-urban), black flying fox (2.99 km urban, 5.27 km non-urban), little red flying fox (7.66 km urban, 13.5 km non-urban), spectacled flying fox (6.70 km urban, 11.8 km non-urban). Data sourced from: grey-headed flying fox<sup>14,15</sup>, black flying fox<sup>14,16</sup>, little red flying fox<sup>14</sup>, spectacled flying fox<sup>17</sup>, topknot pigeon<sup>18</sup>, regent honeyeater<sup>19</sup>, emu<sup>20</sup>, sulphur-crested cockatoo<sup>21</sup>, rainbow lorikeet<sup>22</sup>, musk lorikeet<sup>23</sup>, wompoo fruit-dove<sup>18</sup>, cassowary<sup>24</sup>, red-necked wallaby<sup>25</sup>, common brushtail possum<sup>26</sup>, eastern spinebill<sup>27</sup>.

## Results

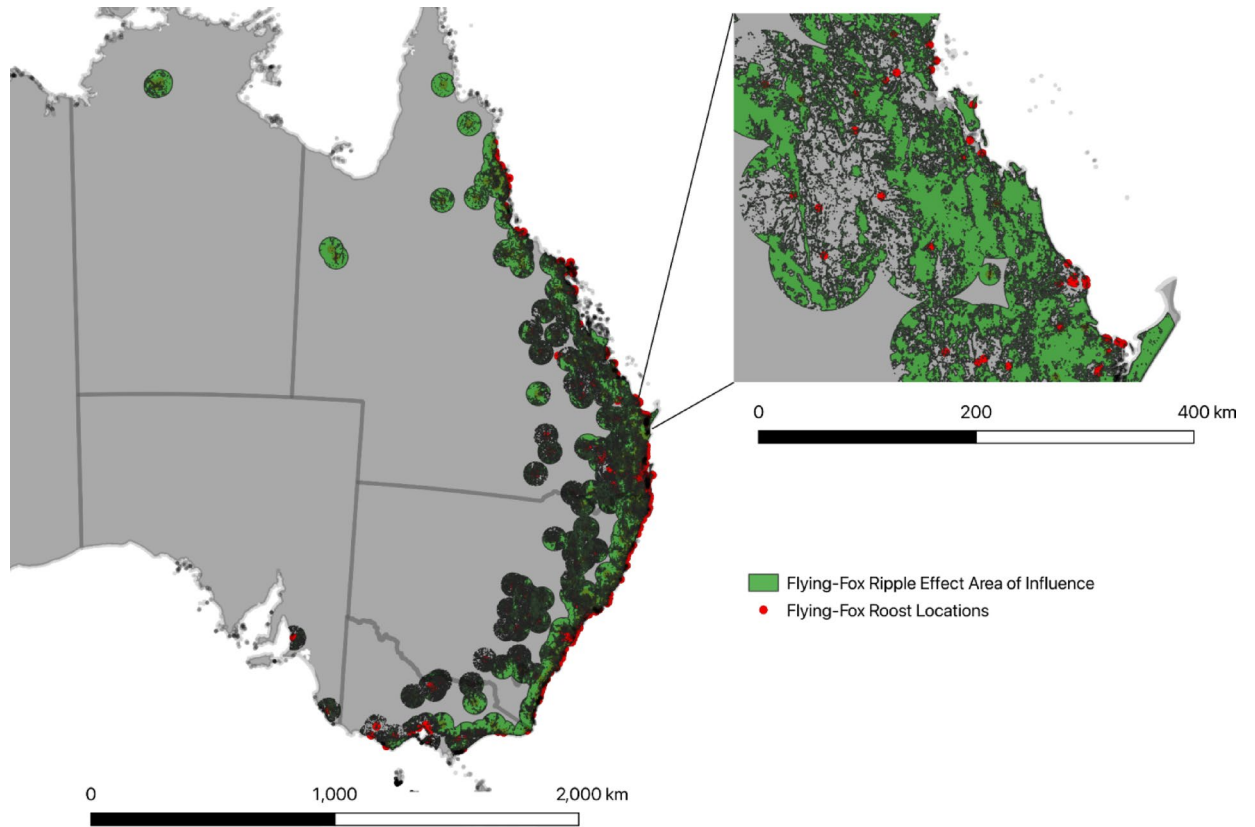
Flying fox roosts' mean buffer areas accounted for 116,252 km<sup>2</sup>. By overlapping the areas flying foxes are likely to use with our mean buffer areas, we obtained a total area of 60,778 km<sup>2</sup>. For maximum flight distances across the four species, the maximum buffer area increased to 698,549–414,230 km<sup>2</sup> when overlapped with areas flying foxes are likely to use (Fig. 2).

The total overlap of *P. poliocephalus* with Australia's timber industry area was 36,038 km<sup>2</sup>. The estimated median economic contribution of *P. poliocephalus* pollination to the Australian eucalypt timber industry was AUD \$611 million per year, with a 90% uncertainty interval ranging from AUD \$271 million to AUD \$955 million per year (Fig. 3). One-way sensitivity analysis showed proportional responses of the model to changes in the pollination dependence ratio (PDR). Reducing the mean PDR by 50% lowered the median estimate to AUD \$303 million (5–95%: AUD \$0–649 million), whereas increasing the PDR by 50% raised it to AUD \$918 million (5–95%: AUD \$578 million–1.16 billion) (Supplementary Table 1).

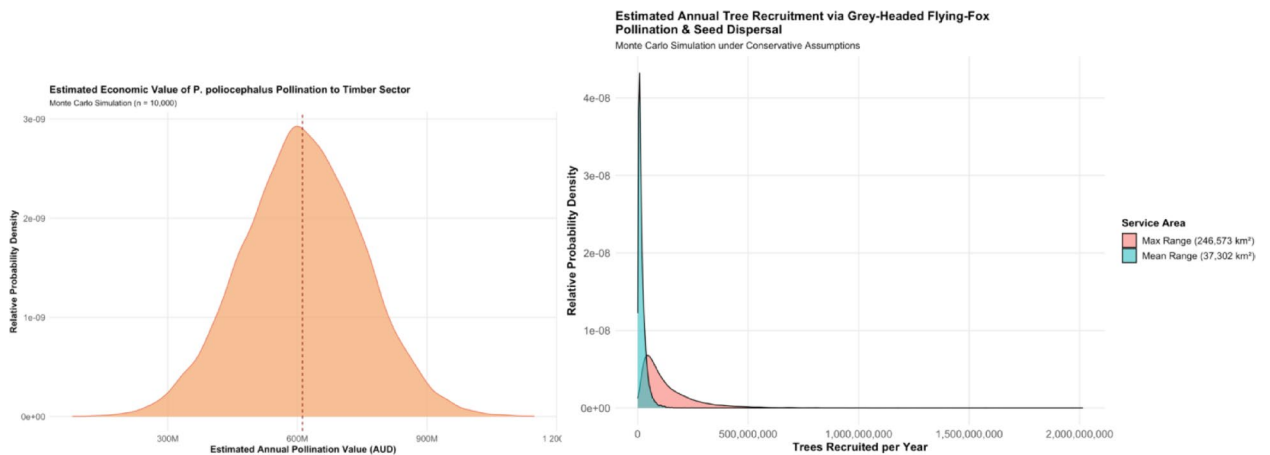
Under conservative assumptions, *P. poliocephalus* is estimated to facilitate the recruitment of a median of 13.9 million trees per year within their mean foraging range (37,302 km<sup>2</sup>), and 91.6 million trees per year across their maximum ecological service range (246,573 km<sup>2</sup>) (Fig. 3). Even in constrained scenarios, annual recruitment remained substantial, with 90% uncertainty intervals ranging from 3.1 to 57.2 million trees in the mean area and 20.4 to 378.2 million trees in the maximum area. One-way sensitivity analysis showed that total recruitment was only weakly affected by uncertainty in the pollination pathway ( $\pm 50\%$  changes in pollination success altered median recruitment by < 3% for both ranges), but strongly sensitive to assumptions about seed load: a  $\pm 50\%$  change in effective seed load produced  $\sim \pm 47\%$  changes in median recruitment, from 7.3 to 20.4 million trees in the mean range and 48.2 to 134.6 million trees in the max range (Supplementary Table 2).

## Discussion

Flying foxes occupy an important ecological role as dispersers and pollinators in the Australian landscape, a role our estimations strongly reinforce. Our study estimates that Australia's Bat Ripple—the radiating service area of Australia's flying fox populations—spans 11.6–41.4 million hectares, an area equivalent to the size of Sweden or about quarter the size of Queensland (41.4 million ha at the upper bound). This area underscores their capacity to influence ecosystem dynamics, for example through pollination and seed dispersal of important plant species, across native forests, timber plantations, and potential reforestation areas. Within their maximum nightly foraging area, *P. poliocephalus* alone facilitates an estimated 20.4–378.2 million new trees annually (90% SI), highlighting their contribution to forest regeneration and long-distance gene flow across fragmented landscapes.



**Fig. 2.** Total estimated Bat Ripple area of influence of 414,230 km<sup>2</sup>, representing the maximum nightly foraging range of all four flying-fox species buffered around 1,209 known roost locations across continental Australia. Map generated in QGIS 3.26 Buenos Aires (QGIS Association, <https://qgis.org>).



**Fig. 3.** Results of Monte Carlo simulations ( $n = 10,000$ ) for (a) the estimated annual economic value of *P. poliocephalus* pollination to the Australian eucalypt timber sector and (b) the estimated annual tree recruitment attributable to the *P. poliocephalus* population via pollination and seed dispersal. Panel (a) shows the probability density of pollination value, with an estimated median of approximately AUD \$611 million and a 90% uncertainty interval of AUD \$271–955 million. Panel (b) shows that estimated tree recruitment has a median of 13.9 million trees per year within the mean foraging area (37,302 km<sup>2</sup>) and 91.6 million trees per year across the maximum ecological service area (246,573 km<sup>2</sup>), with 90% uncertainty intervals of 3.1–57.2 million and 20.4–378.2 million trees, respectively, under conservative assumptions.

We acknowledge that quantitative data on flying fox diet composition (particularly for the lesser studied *P. alecto*, *P. scapulatus*, and *P. conspicillatus*), visitation rates and fine-scale foraging behaviour remain limited, especially across the full diversity of fruit species they use, both native and non-native, and given their behaviour as a nomadic species. Our tree recruitment model therefore relies on a representative fig assemblage and conservative estimates and parameter ranges (see Supplementary Information 1). Our sensitivity analysis shows that, although total recruitment is sensitive to assumptions on seed load, even halving the effective seed load still yields tens of millions of recruits annually across the maximum service area (Supplementary Table 2). Taken together, these results suggest that, even under conservative and data-limited assumptions, *P. poliocephalus* likely play a major and spatially extensive role in maintaining forest structure and connectivity in eastern Australia.

Economically, we estimate that flying fox pollination services contribute between AUD \$ 271 million and 955 million per year to the Australian eucalypt timber industry. While the profitability of the native forest sector remains debated<sup>28</sup>, our focus is on the ecological significance of flying foxes. Although many taxa contribute to pollination<sup>29</sup>, flying foxes play a distinct role due to their long-distance pollen transport (Fig. 1). We recognize that pollination systems are often nonlinear and may exhibit functional redundancy; additionally, as our sensitivity analysis shows, our estimated values scale with the PDR but remain in the hundreds of millions of AUD even under conservative PDR assumptions. However, bats contribute uniquely to long-distance gene flow and pollination quality, rather than just quantity, functions that are less easily replaced<sup>30</sup>. Bat pollination has evolved repeatedly across plant lineages, with more than 500 species adapting floral traits to attract bats as efficient and far-reaching pollinators<sup>31</sup>. Unlike birds or insects, bats have a greater capacity to carry and deposit large amounts of pollen in each visit, reinforcing their role as high-efficiency pollinators, especially in tropical and subtropical systems<sup>32</sup>. While declines in flying fox populations may not immediately impact timber yields, the erosion of pollination quality presents a delayed yet serious risk to forest regeneration and adaptability.

The potential loss of this Bat Ripple effect would potentially be of profound ecological importance. Their population decline could reduce pollination quality, limit tree recruitment, and constrain long-term forest productivity; particularly under intensifying climate stress<sup>6</sup>. Their absence would disrupt both seed dispersal and pollination networks, leading to cascading effects on forest structure and biodiversity<sup>33</sup>. Beyond timber productivity, flying foxes also support Australia's climate mitigation goals<sup>31</sup>. By facilitating recruitment, they indirectly promote carbon sequestration in both standing biomass and durable wood products. Australia's forests store over 10.5 billion tonnes of carbon, with an additional 148.5 million tonnes held in wood products and landfills<sup>34</sup>. Moreover, the pollination and seed dispersal services we estimate represent only part of the wider array of ecosystem functions bats perform; flying foxes, like other bat species, also contribute to pest control, nutrient cycling, and even cultural and economic services through guano production and tourism; benefits that remain unaccounted for in our models<sup>35</sup>. This aligns with the principle that conserving functional wildlife—such as flying foxes—within plantation landscapes is essential to sustaining long-term ecosystem processes<sup>36</sup>. Our estimates, therefore, likely represent a conservative lower bound of the true value flying foxes bring to Australian landscapes.

Our results align with recent studies that have assigned similar valuations to flying fox ecosystem services in Southeast Asia<sup>9</sup>, Madagascar<sup>37</sup>, West Africa<sup>8</sup>, and Indonesia<sup>38</sup>, which have underscored the important economic and ecosystem services flying foxes provide. However, our analysis faces limitations due to data gaps, particularly in quantifying tree visitations, dispersal events per night, diet composition, and seed dispersal distances. These recruitment estimates should be interpreted as approximations rather than actual measured values based on conservative ecological assumptions and limited by the current absence of species-specific pollination and regeneration data, and by the simplifying assumption that services are delivered relatively uniformly across the species' foraging range, despite the underlying spatial and temporal heterogeneity in resource distribution. Despite these constraints, our conservative range, grounded in the available ecological data, estimates, and equivalences, demonstrates the immense value these species bring to Australia's economy and environment, and is likely an underestimate: the model only considers *P. poliocephalus* out of the four species present in mainland Australia which likely contribute greatly to these services. Furthermore, historical declines, especially of the endangered spectacled flying fox whose populations may be at a "tipping point"<sup>39</sup> signal an urgent need for conservation action to protect these important long-distance dispersers and their contributions to ecosystem and climate resilience. Together, these scenario-based estimates provide an initial quantitative benchmark that can be used by policymakers and businesses to explicitly recognise and incorporate flying fox-mediated ecosystem services into conservation planning and economic decision-making. More broadly, our study is intended as a starting point for valuing and communicating the importance of flying foxes in Australian ecosystems, with the aim of elevating their conservation priority. Future research should focus on refining dispersal and pollination event data to further illuminate the full scope of their ecological impact.

## Methods

### Land use classification

Land use data were obtained from the Australian Collaborative Land Use and Management Program (ACLUMP), provided by the Department of Agriculture, Fisheries and Forestry (ABARES) (<https://www.agriculture.gov.au/abares/aclump/land-use/data-download>). Raster land use data were reclassified and vectorized to enable spatial analysis. For this study, we selected the following land use categories as representative of areas flying foxes are likely to use: nature conservation, managed resource protection, other minimal use, production native forests, grazing native vegetation, and plantation forest. These classifications reflect a combination of protected, minimally disturbed, and forested environments used by flying foxes for roosting or foraging.

### Flying fox roost location data and classification

For this continent-wide estimation, we used roost location data for the four species of Australian flying foxes obtained from the Commonwealth Scientific and Industrial Research Organization (CSIRO) National Flying-Fox Monitoring Program database<sup>40</sup>. The listed roosts are locations confirmed through direct visual observations by CSIRO, state and local governments and volunteer groups as current or past colonies of flying foxes and have been compiled through quarterly surveys conducted between 2012 and 2022. Roost data were cleaned and filtered to include only those classified as Class 1, 2, or 3, based on the methodology described by Vanderduys et al.<sup>41</sup>. A total of 1,209 unique roost locations were retained for spatial analysis: 465 for *Pteropus poliocephalus*, 435 for *Pteropus alecto*, 255 for *Pteropus scapulatus*, and 54 for *Pteropus conspicillatus*. As part of a conservative approach, Class 0 roosts—defined as sites where bats had been historically observed, but never during the survey period—were excluded from our analysis. Surveys were only conducted from 2012 to 2022 prioritizing counting on classes 3 and 2, and it is extremely likely that many roosts remain unknown or have formed more recently, especially in remote or under-surveyed regions. Therefore, our analysis represents a rigorous yet conservative estimate of roost distribution based on the best available data in Australia. Roosts were classified as either urban or non-urban based on their spatial overlap with areas categorized as “urban residential” in national land use datasets. This distinction was included because existing literature suggests that flying foxes in urban environments tend to forage over shorter distances possibly due to the availability of anthropogenic food sources<sup>15,42</sup>.

### Foraging movement radii and buffer zones

To estimate the landscape-level influence of flying fox roosts, we created species- and context-specific buffer zones around each known roost site. These buffers were based on mean and maximum foraging distances per night reported in the literature, with separate values for urban and non-urban roosts. Data on the movement ecology of flying foxes remain limited, particularly for *P. conspicillatus* and *P. scapulatus*. However, available research suggests that flying foxes exhibit high levels of nomadism, capable of travelling thousands of kilometers annually in search of flowering and fruiting resources<sup>14</sup>. As data remains limited, the distinction for spatial use between urban and non-urban use was extrapolated as the proportion established for *P. poliocephalus* for the other three species<sup>15</sup>. For the *P. poliocephalus*, mean urban buffers were set at 6.78 km and non-urban buffers at 11.94 km<sup>15</sup>, with a maximum of 50 km<sup>43</sup>. For the *P. alecto* buffers used in urban and non-urban areas was a mean of 2.99 km and 5.27 km respectively<sup>14,16</sup> with a maximum foraging distance of 9.95 km. *P. scapulatus* buffers were 7.66 km and 13.5 km respectively for urban and non-urban areas<sup>14</sup> with a maximum foraging distance of 50 km. *P. conspicillatus* buffers were 6.70 km and 11.8 km for urban and non-urban respectively<sup>17</sup> with a reported maximum of 43.4 km<sup>17</sup>. Two estimates for the *Bat Ripple* were generated for each roost: one using the mean urban and non-urban foraging distances described above, and a second using the maximum foraging distances reported for each species. All buffers were spatially dissolved into continuous polygons to represent the overall area of potential influence. These polygons were then intersected with selected land use categories to estimate the extent of the area within the flying fox species foraging ranges.

### Overview of modelling approach

We developed two probabilistic Monte Carlo models to estimate (1) the annual economic value of *Pteropus poliocephalus* pollination in the Australian eucalypt timber industry, and (2) the contribution of *Pteropus poliocephalus* to landscape-scale tree recruitment via pollination and seed dispersal. Both models applied conservative ecological assumptions and parameter distributions informed by empirical literature. Simulations were conducted over 10,000 iterations in R (v4.1.0) to capture uncertainty in ecological processes and species-specific behaviours.

For the economic valuation, annual pollination value was calculated as:

$$\text{Pollination Service Value(AUD)} = \text{PDR} \times \text{Per ha Timber Value} \times \text{Bat Service Area(ha)}$$

where the pollination dependence ratio (PDR) represents the proportion of plant production attributable to animal pollination. In the absence of timber-specific and *P. poliocephalus* PDR estimates, we parameterised PDR as a normal distribution (mean=0.58, sd=0.18) derived from empirical studies of bat-pollinated crop systems<sup>9,44–47</sup>, and defined bat service area using our GIS-based estimate of the *P. poliocephalus* foraging extent.

For the tree recruitment model, we used the estimated *P. poliocephalus* population (578,350 individuals (s.e. ± 24,450)<sup>41</sup> and partitioned 300 active nights per year between flower foraging and frugivory, then estimated trees recruited via pollination as:

$$\text{Pollination Tree Recruitment} = \text{Bat population} \times \text{Pollination success rate} \times \text{Flower foraging nights}$$

with pollination success given by the estimated product of floral encounters, pollination probability, seedling establishment and recruitment probabilities (details provided in Supplementary Information 1). In parallel, seed-dispersal-driven recruitment was estimated from nightly fruit intake on a representative fig assemblage (*Ficus coronata*, *F. fraseri*, *F. macrophylla*) found commonly in the diet of *P. poliocephalus*<sup>48</sup>, using distributions for fig mass, effective seed load, proportion of seeds ingested, and per-seed germination, establishment and recruitment<sup>37,48,49</sup>, scaled to the population and service area and summed with the pollination pathway for both mean and maximum foraging ranges. A detailed description of model equations, parameter values and sources, and the one-way sensitivity analysis on PDR/pollination success and seed load is provided in Supplementary Information 1.

## Data availability

Roost location and abundance data for Australian flying-foxes were obtained from the CSIRO National Flying-Fox Monitoring Program and are available via the program's data portal as described in McKeown, Vanderduys, & Westcott. 2024 (<https://data.csiro.au/collection/csiro%3A64370v3>). Land-use and forest/plantation layers used in the analyses were sourced from ABARES, including the National Forest Inventory and national land use datasets (<https://www.agriculture.gov.au/abares/acump/land-use/data-download>). All derived data and code is available on: <https://github.com/AlfredoOrtega22/The-Bat-Ripple-Effect-Code>.

Received: 2 September 2025; Accepted: 2 February 2026

Published online: 24 March 2026

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### Author contributions

A.O.G. and A.B. contributed to the conceptualization, data analysis, and writing of the manuscript. H.P., D.B., and N.A. contributed to manuscript editing, data interpretation, and critical revisions. All authors reviewed and approved the final version of the manuscript.

### Funding

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

### Declarations

### Competing Interests

The authors declare no competing interests.

### Additional information

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1038/s41598-026-39042-0>.

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