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Large urban trees are keystone structures for Australian microbats

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ABSTRACT

Large trees are keystone structures for a range of taxa. Insectivorous bats depend on large trees for roosting habitat, such as hollows and peeling bark, as well as habitat for their prey. However, large trees are in decline in urban areas globally. We sought to determine if the richness and activity of insectivorous bats in urban environments is associated with the occurrence of large trees; and in which urban landscape context large trees have greatest benefit for insectivorous bats. Using ultrasonic bat detectors set at 83 sites spanning temperate and subtropical cities in eastern Australia, we identified 20,026 bat passes from 16 microbat species and four species complexes. We found strong positive associations between four bat metrics (mean nightly activity, richness and activity of edge-adapted bats and vespertilionid bat activity) and the number of large trees ≥50 cm DBH. We also found evidence that large trees supported a higher richness of edge-adapted bats in areas with lower woody vegetation cover. Our data indicate that the value of large trees for edge-adapted bats is enhanced when large trees are isolated – a relationship previously demonstrated for birds but not bats. Large trees in urban greenspace, especially trees in isolation, offer valuable habitat that supports a substantial community of insectivorous bats. Our results highlight the importance of retaining large, isolated trees (both native and non-native) in urban greenspace for bat conservation.

1. Introduction

Large trees are keystone structures for a broad range of taxa (Fischer et al., 2010; Manning et al., 2006; Parsons et al., 2025; Stagoll et al., 2012). Large trees provide a range of ecosystem services and resources for fauna that are either unavailable or in lower quantity in younger, smaller trees (e.g. hollows, preferred perching branches, large quantities of nectar or fruit) (Gibbons and Lindenmayer, 2002; Hall and Bunce, 2011; Holland et al., 2024; Le Roux et al., 2014; Lindenmayer et al., 2014; Remm and Lõhmus, 2011). In urban environments, large trees act as stepping stones, facilitating movement of fauna that otherwise may not persist in fragmented habitats (Lapin et al., 2024; Le Roux et al., 2015; Le Roux et al., 2017).

Large trees are in decline across urban areas globally (Canetti et al., 2018; Li et al., 2022; Parsons et al., 2023; Paul et al., 2021). In urban environments, large trees are typically retained only where they occur in patches of remnant vegetation (Parsons et al., 2023). This pattern of retention is likely due to two key reasons: the perceived difficulty to maintain safe separation between large trees and 'targets' (i.e., people and infrastructure); and the notion that small and isolated habitats (including large trees) are not considered to have the same benefits for wildlife as larger, more connected habitats. However, scattered or isolated large trees can be disproportionately valuable for mobile fauna (e.g., bats and birds) in modified landscapes compared to trees in large forest remnants (Crane et al., 2014; Law et al., 2000; Le Roux et al., 2017; Parsons et al., 2025). The habitat value of scattered trees and fragmented habitat patches are often overlooked by conservation efforts (Hanspach et al., 2011; Manning et al., 2006; Soanes et al., 2019).

Relationships between insectivorous bat activity and large trees across the urban matrix are varied (Dietz et al., 2020). The presence of large trees and tree networks can help alleviate the pressure of increasing urbanisation (Hale et al., 2012). Threlfall et al. (2016), in a study of urban greenspace in Melbourne, Australia, reported that an increase in density of trees >41 cm diameter at breast height (DBH) was

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related to a positive response in bat species richness. Additionally, they reported significantly higher total activity, and activity of edge-adapted bats with an increased density of trees >81 cm DBH (Threlfall et al., 2016). Conversely, a study from the ACT, Australia, found no significant effect of tree size on bat activity, richness or community composition (Le Roux et al., 2017). Le Roux et al. (2017) also reported that while insectivorous bat activity and richness was significantly reduced at trees in urban built-up areas, bat richness at trees in urban parks was similar to trees in pasture or nature reserves. Outside of the work of Le Roux et al. (2017), little research has been conducted on the relationship between large trees and bat activity in different urban contexts.

Relationships between insectivorous bats and tree cover are varied in disturbed environments (Hale et al., 2012; Law et al., 2011; Moretto et al., 2019; Wentzel et al., 2019). In agricultural landscapes, foraging activity at individual scattered trees is reportedly similar to foraging activity at trees within patches of remnant vegetation (Lumsden and Bennett, 2005). Across the urban matrix, a Canadian study reported that insectivorous bat activity increased by 44 % for each 10 % increase in tree cover (Moretto et al., 2019). Interestingly, while Bailey et al. (2019) reported negligible effects of urban development on the occurrence of all insectivorous bat species, they also noted that the occurrence of smaller, edge-adapted vespertilionid species responded positively to 50 % increases in canopy cover, while a larger, open-adapted species (*Tadarida brasiliensis*) responded negatively to increasing canopy cover.

While some bat species can thrive in urban environments, many species are less tolerant of human activities and are negatively impacted by habitat degradation, noise pollution and light pollution associated with urban developments (Caryl et al., 2016; Coleman and Barclay, 2011; Haddock et al., 2019; Krauel and LeBuhn, 2016; Le Roux et al., 2017; Luck et al., 2013). Urban environments present novel opportunities for insectivorous bats, with some edge-adapted species adept at benefitting from the increased insect activity under urban lighting, while some open-adapted bats with less manoeuvrability are impacted negatively by that same situation (Li and Wilkins, 2022; Villarroya-Villalba et al., 2021). Many of the species persisting in urban environments have adapted to roosting in urban structures, including buildings, bridges, road culverts, artificial nest boxes and even pool umbrellas (Godinho et al., 2020; Gorecki et al., 2020; Griffiths et al., 2017; Maltby et al., 2010; Rhodes and Jones, 2011).

In this study we seek to improve the current understanding of microbat activity in urban environments by exploring a range of bat community metrics across two contrasting areas of Australia: South East Queensland characterised by subtropical sclerophyll forest fragments, and the Australian Capital Territory characterised by temperate grassy woodlands. To address this aim, we posed two research questions: (1) is the richness and activity of insectivorous bats in urban environments associated with the occurrence of large trees; and (2) what is the landscape context in which large trees have greatest benefit for insectivorous bats in urban environments? We refer to vegetation in the surrounding area as landscape context. The difference in biota and climate are likely to drive a lot of the variation in species richness and activity, and thus we focused more on the within region variation than between regions.

2. Methods

2.1. Study area

We selected sites across two distinct urban regions of Australia, the Australian Capital Territory (ACT), and South East Queensland (SEQ). Canberra in the ACT, supports a population of 457,000 people (Australian Bureau of Statistics, 2023). The ACT has a temperate climate with approximately 625 mm of average annual rainfall, and mean annual temperatures around 20–22 °C. The green spaces of ACT's urban matrix range from patches of temperate grassy woodlands to previously cleared agricultural landscapes. Tree cover in the ACT varied from patches of remnant native trees, to scattered native trees, to planted non-native trees. South East Queensland (SEQ), incorporating the cities of Brisbane and the Gold Coast, supports 3.80 million people (Australian Bureau of Statistics, 2023). SEQ has a subtropical climate, with approximately 1500 mm of average annual rainfall, and mean annual temperatures around 25–27 °C. The urban matrix of SEQ is a highly modified landscape consisting of greenspace varying from remnant or regrowth bushland patches to small patches or strips of sclerophyll forest to turfed parks. Tree cover in SEQ was generally native trees, occurring where planted, or as remnant trees in isolation or as part of remnant or regrowth vegetation. Urban greenspace in both regions consist of predominantly native vegetation. Both regions had predominantly native tree species from the genus *Eucalyptus*, with SEQ sites also having a presence of *Corymbia*, *Ficus*, *Lophostemon*, *Melaleuca*, and *Casuarina/Allocasuarina*. Some sites in the ACT also had non-native trees present from the *Acer* genus.

2.2. Site selection

We selected a total of 83 sites (ACT $n = 43$, SEQ $n = 40$) from urban greenspace located within residential developments established between 2005 and 2021. Large trees are almost exclusively retained in patches of remnant vegetation or parklands, rather than on private blocks or as street trees (Parsons et al., 2023). To sample urban greenspace with retained trees, we selected patches of remnant vegetation and urban green spaces located within 50 m of an urban development or roadway on at least two sides (see Plate 1 for examples). We selected sites to represent different densities of mature trees and vegetation cover. Sites were on average 1207 m apart (range 250–8340 m). We defined sites as a 50 m radius circle, or on two occasions, a rectangular shape of an equivalent area where the site was too narrow to accommodate the full circle.

2.3. Bat surveys

We recorded insectivorous bat activity and species richness using ultrasonic bat detectors (Anabat Express) (Titley Scientific, 2020). We set two detectors per site, recording on nights only (30 min before sunset until 30 min after sunrise), for a minimum of three consecutive nights. We set each of the two detectors to record bat activity over the same consecutive nights at each site. We used two detectors per site to maximise the likelihood of recording all bats travelling through the 50 m radius site, particularly given the potential noise interference from urban disturbance and the close range of detection for the bat detectors. Recording took place over spring and early summer, with detectors running from November 2021 to January 2022 for ACT sites, and September to November 2021 for SEQ sites. We aimed to set the detectors on the trunks of large trees where possible, using smaller trees or posts if no trees were available, secured at approximately 1.7–2.5 m above the ground. Each omnidirectional microphone had an extension cable that allowed it to be angled out 45 degrees from horizontal, positioned to face gaps in vegetation or structural clutter. We set detectors at a minimum of 30 m apart from each other, and angled the detectors to face in different directions from each other.

The ultrasonic detectors record all zero-crossing data over a 24-hour period as compilation files (.zca) (Titley Scientific, 2020). To clean the data, we began with all 674 survey replicates (i.e., two detectors per site, each recording for three to seven nights). We removed survey replicates ($n = 30$) where zero data were recorded as a result of technical issues. We used AnalookW software (Corben, 2021) to separate each file into separate bat passes. Each segment of a microbat call is referred to as a pulse. We set Anascheme to require bat passes to have a minimum of five successive pulses to be identified positively to a given bat species. We used Anascheme software to identify a total of 31,160 bat passes (Adams et al., 2010). However, only bat passes with >50 % confidence of species identification by Anascheme ($n = 20,026$) were used for analyses. We used the North Coast key for the ACT data, and the Upper North Coast

Plate 1. Top photos show site SEQ-09, bottom photos show site ACT-39. Aerial images show 50 m radius circle in red indicating site extent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

NSW/SEQ regional key for the SEQ data. Species identification was manually checked using call identification manuals (Pennay et al., 2004; Reinhold et al., 2001). We manually checked a selection of calls for each species, and re-assigned calls to a complex or the correct species as appropriate. However, not every individual call was manually checked, and Anascheme has varying levels of confidence depending on the species and settings. The settings we have described can allow for reasonable confidence with the identifications, however, for certain species such as *Chalinolobus nigrogresius*, the confidence is reduced (Adams et al., 2010). We assigned calls to four species complexes where calls recorded were not able to be differentiated to the species level acoustically: the *Ozimops* species complex (*O. planiceps* and *O. ridei*), the *Nyctophilus* species complex (*N. gouldi* and *N. geoffroyi*), the *Scotorepens* species complex (*S. greyii* and *Scotorepens* sp. (Parnaby)) (Reinhold et al., 2001; Van Dyck and Strahan, 2008), and the *Vespadelus* species complex (*V. darlingtoni* and *V. regulus*). Some calls for *O. planiceps* and for *O. ridei* were able to be differentiated acoustically to the species level, but where the calls were recorded at the shared characteristic frequency in the ACT, those calls were assigned to the *Ozimops* species complex.

2.4. Bat metrics

We used seven bat community metrics as response variables in our analyses (see Table 1). When conducting our analyses, we used the data collected per survey replicate (i.e., per detector/night/site). The resulting model output for each metric is reported as a mean nightly value. To calculate these metrics, we separated each bat species by their flight style adaptation: open-adapted, edge-adapted or narrow-space (Churchill, 2008; Jung and Threlfall, 2018) (Table 2). Within our study, we recorded two bat families as open-adapted (Emballonuridae and Molossidae), and two families as edge-adapted (Miniopteridae and Vespertilionidae). One species complex, the *Nyctophilus* complex within the Vespertilionidae family, was the only recorded species/complex to use a narrow-space adapted flight style. As the recorded activity of the *Nyctophilus* complex was very low (<100 calls total), narrow-space adapted bat activity was not modelled. We chose to model activity for vespertilionid bats given they were the most speciose family, as well as facilitating the separation of forest bats from the cave-dwelling miniopterids (Churchill, 2008). In the ACT, two *Ozimops* species (*O. planiceps* or *O. ridei*) could be identified, however their calls did overlap in part, thus resulting in the *Ozimops* complex. We included the *Ozimops* complex as counting toward species richness only when both species weren't identified separately.

Table 1
Definition of each bat metric assessed during model testing.

Bat metric	Definition
Mean species richness	The mean number of microbat species or species complexes recorded in one detector night.
Mean nightly activity	The mean number of passes across all species or species complexes recorded in one detector night.
Edge-adapted bat richness	The mean number of edge-adapted bat species or species complexes recorded in one detector night.
Edge-adapted bat activity	The mean number of passes across edge-adapted species or species complexes recorded in one detector night.
Open-adapted bat richness	The mean number of open-adapted bat species or species complexes recorded in one detector night.
Open-adapted bat activity	The mean number of passes across open-adapted species or species complexes recorded in one detector night.
Vespertilionid bat activity	The mean number of passes across bat species or species complexes recorded from the Vespertilionidae family in one detector night.

As part of reporting on the bat community present in each region, we also sought to determine what percentage of known bat species were recorded, and which of those bats are more sensitive to urbanisation. We have included the available urban sensitivity ratings for the bat species we recorded, as per the work of Threlfall et al. (2012).

2.5. Habitat covariates

At each site, we counted all trees (inclusive of native and non-native) according to DBH class: 11–20 cm, 21–30 cm, etc. up to >90 cm. We measured the DBH for all trees of a minimum 40 cm DBH. For statistical models, we sorted trees into size class bins of a minimum DBH and higher, e.g. ≥40 cm DBH, ≥50 cm DBH, etc. We selected 40 cm DBH as

Table 2
All bat species detected, including their conservation status, flight style, urban sensitivity rating and detection statistics.

Family	Species	Common name	Conservation status	Flight style	Urban sensitivity	Core roosting habitat	No. sites detected (percentage of sites)		Total passes		Mean passes per detector night ± SE	
			IUCN Red List				ACT	SEQ	ACT	SEQ	ACT	SEQ
Emballonuridae	*Saccolaimus flaviventris*	Yellow-bellied Sheath-tailed Bat	LC, Dec	OA		Tree hollows		9 (22.5 %)		17		0.1 ± 0.0
Miniopteridae	*Miniopterus australis*	Little Bentwing Bat	LC, Sta	EA		Caves		24 (60.0 %)		196		0.8 ± 0.2
Miniopteridae	*Miniopterus orianae oceanensis*	Eastern Bentwing Bat		EA	Tolerant	Caves	20 (46.5 %)	20 (50.0 %)	682	56	1.7 ± 0.5	0.2 ± 0.1
Molossidae	*Austronomus australis*	White-striped Free-tailed Bat	LC, Dec	OA	Tolerant	Tree hollows	26 (60.5 %)	36 (90.0 %)	82	1653	0.2 ± 0.0	6.8 ± 1.2
Molossidae	*Micronomus norfolkensis*	Eastern Coastal Free-tailed Bat	NT, Dec	OA	Moderate	Tree hollows, bark		37 (92.5 %)		946		3.9 ± 0.9
Molossidae	*Ozimops lumsdenae*	Northern Free-tailed Bat	LC, Dec	OA		Tree hollows		9 (22.5 %)		13		0.1 ± 0.0
Molossidae	*Ozimops planiceps*	Southern Free-tailed Bat	LC, Dec	OA		Tree hollows	37 (86.1 %)		600		1.5 ± 0.2	
Molossidae	*Ozimops ridei*	Eastern Free-tailed Bat	LC, Unk	OA	Tolerant	Tree hollows, bark	24 (55.8 %)	38 (95.0 %)	182	1436	0.5 ± 0.1	5.9 ± 1.0
Molossidae	*Ozimops* sp. Complex (*O. planiceps* or *O. ridei*)	*Free-tailed Bats*		*OA*		*Tree hollows*	*24 (55.8 %)*		*124*		*0.3 ± 0.0*	
Vespertilionidae	*Chalinolobus gouldii*	Gould's Wattled Bat	LC, Sta	EA	Tolerant	Tree hollows	37 (86.1 %)	39 (97.5 %)	1586	8225	4.0 ± 0.7	33.7 ± 5.8
Vespertilionidae	*Chalinolobus morio*	Chocolate Wattled Bat	LC, Sta	EA	Moderate	Tree hollows, bark	5 (11.6 %)	7 (17.5 %)	12	14	0.0 ± 0.0	0.1 ± 0.0
Vespertilionidae	*Chalinolobus nigrogriseus*	Hoary Wattled Bat	LC, Sta	EA		Tree hollows		35 (87.5 %)		998		4.1 ± 0.8
Vespertilionidae	*Falsistrellus tasmaniensis*	Eastern False Pipistrelle	V, Dec	EA	Sensitive	Tree hollows	5 (11.6 %)		13		0.0 ± 0.0	
Vespertilionidae	*Nyctophilus* sp. complex (*N. geoffroyi* or *N. gouldi*)	*Long-eared Bats*	*LC, Sta LC, Dec*	*NG*	*Moderate*	*Tree hollows, Bark*	*5 (11.6 %)*	*19 (47.5 %)*	*8*	*91*	*0.0 ± 0.0*	*0.4 ± 0.1*
Vespertilionidae	*Scoteanax rueppellii*	Greater Broad-nosed Bat	LC, Sta	EA	Moderate	Tree hollows, bark		3 (7.5 %)		3		0.0 ± 0.0
Vespertilionidae	*Scotorepens orion*	Eastern Broad-nosed Bat	LC, Unk	EA	Moderate	Tree hollows	3 (7.0 %)	7 (17.5 %)	5	32	0.0 ± 0.0	0.1 ± 0.0
Vespertilionidae	*Scotorepens* sp. complex (*S.* sp. (Parnaby) or *S. greyii*)	*Broad-nosed Bats*		*EA*				*28 (70.0 %)*		*1711*		*7.0 ± 1.7*
Vespertilionidae	*Vespadelus* sp. complex (*V. darlingtoni* or *V. regulus*)	*Forest Bats*	*LC, Sta*	*EA*		*Tree hollows*	*27 (62.8 %)*		*986*		*2.5 ± 0.8*	
Vespertilionidae	*Vespadelus pumilus*	Eastern Forest Bat	LC, Sta	EA		Tree hollows		10 (25.0 %)		36		0.1 ± 0.0
Vespertilionidae	*Vespedelus vulturnus*	Little Forest Bat	LC, Dec	EA	Moderate	Tree hollows	19 (44.2 %)		317		0.8 ± 0.2	

Urban sensitivity ratings as per Threlfall et al. (2012). Use of italics outside of scientific name indicates a species complex, wherein the two species cannot be distinguished acoustically. Flight style abbreviations: OA open aerial, EA edge aerial, NG narrow-space/gleaning (Jung and Threlfall, 2018). Conservation status has been reported under the International Union for Conservation of Nature (IUCN Red List) (IUCN, 2024; NSW Gov., 2023). Conservation status abbreviations: LC least concern, NT near threatened, V vulnerable, Dec population decreasing, Sta population stable, Unk population trend unknown.

the minimum threshold for 'large' trees as the same sites were used for our bird focused study (Parsons et al., 2025), following the findings of Stagoll et al. (2012) where they identified trees above 40 cm in DBH had a significant, positive impact on bird fauna in urban parks.

To estimate tree/woody vegetation cover within and around each site, we used ArcGIS Pro to conduct focal statistics for a 200 m radius buffer zone around each site (Esri Inc., 2022). We used a woody vegetation raster (DCCEEW, 2019), derived from Landsat imagery, and mapped at a 25 m spatial resolution, to identify the number of cells containing either woody (minimum 20 % canopy cover of minimum 2 m height and 0.2 ha area) or sparse woody (5–19 % canopy cover) vegetation. We then expressed this value as a percentage of the 200 m buffer and named the variable 'woody vegetation cover'.

2.6. Weather covariates

To account for variation in bat activity and detectability, we recorded three weather covariates. We collected temperature (°C) and wind (km/h) data from the nearest weather station available (Bureau of Meteorology, 2023), in the 9 pm–10 pm time slot. We recorded daily rainfall (mm) as rainfall measured in the 24 h preceding 9 am on the morning following the night of recording (Bureau of Meteorology, 2022).

2.7. Data analysis

To investigate relationships between insectivorous bat community metrics (species richness and activity), region, detection covariates, tree size and woody vegetation cover, we fitted generalised linear mixed models (GLMMs) using the package 'glmmTMB' in R (Brooks et al., 2017; R Core Team, 2023). We interpreted the results using language of evidence, as per Muff et al. (2022). Muff et al. (2022) explains that describing results using a more gradual notion of evidence is a more nuanced approach to reporting statistics than using strict *p*-values. Prior to model fitting we tested the effect the detection covariates had on total bat activity using Akaike's Information Criterion scores with a correction for small sample size (AICc) (Burnham and Anderson, 2002). Model testing showed that daily rainfall and nightly temperature both had strong impacts on total bat activity, and thus were included in all further models as covariates.

We fitted models for the richness of open-adapted bats and the activity of open-adapted bats assuming a negative binomial error distribution with a log-link function. We fitted models for the richness of edge-adapted bats assuming a Poisson error distribution with a log-link function. Preliminary analyses showed that the models for the remaining four metrics demonstrated high probabilities of zero-inflation. We therefore fitted hurdle models assuming a binomial error distribution for the hurdle component of the model and a zero-truncated negative binomial error distribution with a log-link function for the conditional component of the model (Feng, 2021). To allow direct comparisons of effects, we scaled all continuous predictor variables to have a mean of zero and standard deviation of one. To account for spatial autocorrelation, we included a block-level random effect by categorising sites into clusters of spatially close sites (within 2 km of each other). We then added the block as a random intercept factor in all models. This was in addition to the site-level random effect which accounted for repeated measures at the site level and the dependency between two detectors at each site. We combined these random effects by specifying site nested within block as a random effect.

(1) Is the richness and activity of insectivorous bats in urban environments associated with the occurrence of large trees?

To identify if insectivorous bat communities were associated with large trees, we fitted a set of models using each community metric as the response and with region, daily rainfall, temperature, and each large tree size class as predictor variables. We tested five tree size thresholds: ≥40 cm DBH, ≥50 cm DBH, ≥60 cm DBH, ≥70 cm DBH and ≥ 80 cm DBH. We selected the most parsimonious model for each community metric using AICc with a correction for small sample size (Burnham and Anderson, 2002) (Table S1). The model formula for each model set followed the following formula: *Community_Metric* ~ *Tree_Size_Threshold* + *Region* + *Temperature* + *Daily_Rainfall*.

(2) In which landscape context do large trees have greatest benefit for insectivorous bats in urban environments?

To identify if the use of large trees by bats varied with landscape context, we continued GLMM testing using the tree-size threshold with most support for each bat community metric. For each metric we employed multi-model inference to compare five models incorporating region, daily rainfall, temperature, the tree size threshold identified in the previous step, and woody vegetation cover. We selected the most parsimonious model for each community metric using AICc scores with a correction for small sample size (Burnham and Anderson, 2002) (Table S2). Where the interaction model (i.e., model e) was the top-ranked model, we plotted the interactive effect in Fig. 2. We plotted the effect sizes for top-ranked conditional models in Fig. S1 and for top-ranked hurdle models in Fig. S2.

We fitted the following models for each model set:

a) Community_Metric ~ Region + Temperature + Daily_Rainfall
b) Community_Metric ~ Tree_Size_Threshold + Region + Temperature + Daily_Rainfall
c) Community_Metric ~ Woody_Vegetation_Cover + Region + Temperature + Daily_Rainfall
d) Community_Metric ~ Tree_Size_Threshold + Woody_Vegetation_Cover + Region + Temperature + Daily_Rainfall
e) Community_Metric ~ Tree_Size_Threshold* Woody_Vegetation_Cover + Region + Temperature + Daily_Rainfall

3. Results

We recorded a total of 20,026 bat passes that were identified to species/complex level over 644 detector nights. We identified a total of 16 confirmed microbat species and four species complexes across both regions (Table 2). Gould's Wattled Bat (*Chalinolobus gouldii*) was the most recorded bat species in both regions, with 1586 passes recorded in the ACT and 8225 in SEQ.

We recorded a total of 3900 trees (≥10 cm DBH) across 83 sites. Of the 523 trees ≥40 cm DBH we recorded, only nine were non-native. The two urban regions comprised similar total numbers of large trees (≥40 cm DBH; ACT = 260, SEQ = 263), however, the distribution of trees within size classes varied between regions. Trees with DBH ≥40 cm DBH constituted 7.3 % of all trees in ACT sites, and 4.1 % of all trees in SEQ sites, respectively. In the ACT, woody vegetation cover within 200 m ranged from 0 to 35 % with a low mean of 6.4 %, compared to SEQ where woody vegetation cover within 200 m was more evenly distributed between 0 and 89 % in SEQ, with a mean of 40.8 %. Ranges and mean values for tree size variables and woody vegetation cover are presented in Table S3.

In the ACT, 4599 passes were identified to species/complex over a total 400 detector nights. Twelve species/complexes were identified with five species/complexes only recorded in the ACT region in this study (including the *Ozimops* and *Vespadelus* species complexes) (Table 2). The mean number of passes we recorded per survey replicate was 11.5 (range 0–210), and the mean number of passes recorded per site was 107.0 (range 0–1157). After *C. gouldii*, the next most recorded bat species/complexes in the ACT were the *Vespadelus* complex with 986 passes, followed by the Eastern Bentwing Bat (*Miniopterus orianae oceanensis*) at 682 passes.

In SEQ, over three times as many passes as ACT were identified

positively to species/complex at 15,427 identified passes over a period of 244 detector nights. Fifteen species/complexes were identified with eight unique to the SEQ region in this study, including the *Scotorepens* species complex (Table 2). The mean number of passes we recorded per survey replicate was 63.2 (range 0–998), and the mean number of passes recorded per site was 385.7 (range 0–2239). After *C. gouldii*, the species/complex with the second highest activity was the *Scotorepens* species complex with 1711 passes, followed by the White-striped Free-tailed Bat (*Austronomus australis*) at 1653 passes.

We recorded bat species that varied in terms of conservation status, habitat use and adaptability to urban environments (Table 2). Two species are considered Vulnerable or Near Threatened in the IUCN Red List, and eight species were indicating decreasing population trends upon their latest IUCN assessments in 2016 or 2019 (IUCN, 2024). We recorded 12 edge-adapted (i.e., edge aerial) bat species/complexes. We recorded six open-adapted (i.e., open aerial) bat species, including the *Ozimops* complex where both species have been confirmed individually. We recorded one species complex of narrow-space adapted flyers (Jung and Threlfall, 2018). We recorded the presence of four species tolerant to urbanisation, five species and one species complex moderately sensitive to urbanisation, and one species that is very sensitive to urbanisation (Threlfall et al., 2012).

3.1. Is the richness and activity of insectivorous bats in urban environments associated with the occurrence of large trees?

For five of the seven community metrics tested, we found the top-ranked models contained the tree size threshold of trees ≥50 cm DBH (Fig. 1, Fig. S1). Mean nightly activity, activity and richness of edge-adapted bats, and activity of vespertilionid bats all indicated strong evidence for positive associations with the number of trees ≥50 cm DBH (Table S1). Mean species richness indicated weak positive association with the number of trees ≥50 cm DBH. For the remaining two community metrics (richness and activity of open-adapted bats), the null model had the lowest AICc score, followed by the tree size threshold of trees ≥80 cm DBH (scoring within 2 AICc of the null). Daily rainfall had negative associations with all metrics, while temperature had positive associations. All community metrics were recorded at significantly higher values in the region of SEQ compared to the ACT.

Four metrics (mean species richness, mean nightly activity, activity of edge-adapted bats and vespertilionid bat activity) were modelled with hurdle models (Fig. S2). The data revealed strong to very strong evidence that the likelihood of a 'zero' in all four metrics was negatively associated with the number of trees ≥50 cm in DBH (Table S1). That is, at sites with greater numbers of trees ≥50 cm in DBH, the likelihood of detection was increased. The data also revealed very strong evidence that the likelihood of a 'zero' in all four metrics was reduced in the region of SEQ compared to the ACT. There was strong evidence to suggest that daily rainfall increased the likelihood of a 'zero' occurring for all four metrics.

3.2. In which landscape context do large trees have greatest benefit for insectivorous bats in urban environments?

When incorporating landscape context variables into model testing, the model fit improved only for the richness of edge-adapted bats (Fig. 2, Table S2). The top-ranking model for richness of edge-adapted bats included an interaction between trees ≥50 cm in DBH and woody vegetation cover. Predictions from this model indicated that richness of edge-adapted bats increased with the number of trees ≥50 cm in DBH, with greater richness associated with large trees occurring in areas with less woody vegetation cover (Fig. 2).

4. Discussion

Over 644 detector nights in urban greenspaces across two distinct cities in eastern Australia, we recorded 20,026 bat passes that were identified to 16 microbat species and four species complexes. We provide strong evidence that four bat community metrics, including mean nightly activity, responded positively to increasing numbers of large trees (≥50 cm DBH). We also observed that the activity of edge-adapted bats was strongly positively associated with large trees in urban areas, while the activity of open-adapted bats was weakly positively associated. Furthermore, we found that large trees supported a higher richness of edge-adapted bats in areas with lower woody vegetation cover. This novel finding highlights the importance of scattered trees for microbat conservation.

4.1. Is the richness and activity of insectivorous bats in urban environments associated with the occurrence of large trees?

We observed positive associations between five measures of the bat community and increasing numbers of large trees (DBH ≥50 cm). There was strong evidence to support that mean nightly activity increased with an increasing number of large trees, as did richness and activity of edge-adapted bats and activity of vespertilionid bats. There was weak evidence to support the positive relationships between increasing numbers of trees of DBH ≥50 cm and mean species richness. We tested different DBH size thresholds, and trees with a DBH ≥50 cm consistently had the greatest impact on the bat community across temperate and sub-tropical urban landscapes. While several studies have explored the relationship between the size of large trees and roosting activities of bats, few studies have assessed the relationship for community metrics and overall bat activity (Hourigan, 2009; Hourigan et al., 2010). In a study from urban areas in Austria, Suarez-Rubio et al. (2018) reported a positive relationship between DBH of trees >30 cm and total bat activity. In a study from urban areas in Melbourne, Australia, Threlfall et al. (2016) found that an increased density of trees >41 cm in DBH related positively to all bat metrics they tested. They also reported that activity for all bats and for edge-adapted bats increased significantly when the density of trees >81 cm in DBH increased. Conversely, Le Roux et al. (2017) did not observe a significant effect of tree size on bat richness or activity. While their study was also conducted in the ACT, Le Roux et al. (2017) were testing effects of individual trees on the metrics of total bat richness, relative activity, and assemblage in urban, agricultural and uncleared landscapes. Given our different metrics tested, and the impacts of assessing a site-based community versus a tree-based community, this could explain the differences observed between their study and ours (Le Roux et al., 2017).

Our results provide support for retaining and protecting large trees ≥50 cm in urban environments. Large trees are vital for insectivorous bats globally as they provide habitat for the bats and for their insect prey. We recorded 19 bat species (including those within complexes) known to use tree hollows or bark as roosting habitat (Churchill, 2008). Most of these species prefer to use hollows in large, mature, or dead trees for their roosts, with some species exclusively using such trees (Burgar et al., 2015; Churchill, 2008; McConville and Law, 2013; Rhodes and Wardell-Johnson, 2006; Threlfall et al., 2013). Large trees have greater capacity for deadwood, more decorticating bark, more cavities and more opportunities for decay and insect activity, thus increasing prey availability for insectivorous bats (Bar-Ness et al., 2012; Basile et al., 2020; Gibbons et al., 2000; Holland et al., 2024; Law et al., 2011; Lindenmayer et al., 2018).

4.2. In which landscape context do large trees have greatest benefit for insectivorous bats in urban environments?

Once we identified a tree size threshold for effects on bat metrics, we sought to determine if the tree size effect differs by landscape context. For total bat richness, total bat activity, activity of edge-adapted bats, and activity of vespertilionid bats, the presence of large trees was the most important predictor, regardless of woody vegetation cover within a

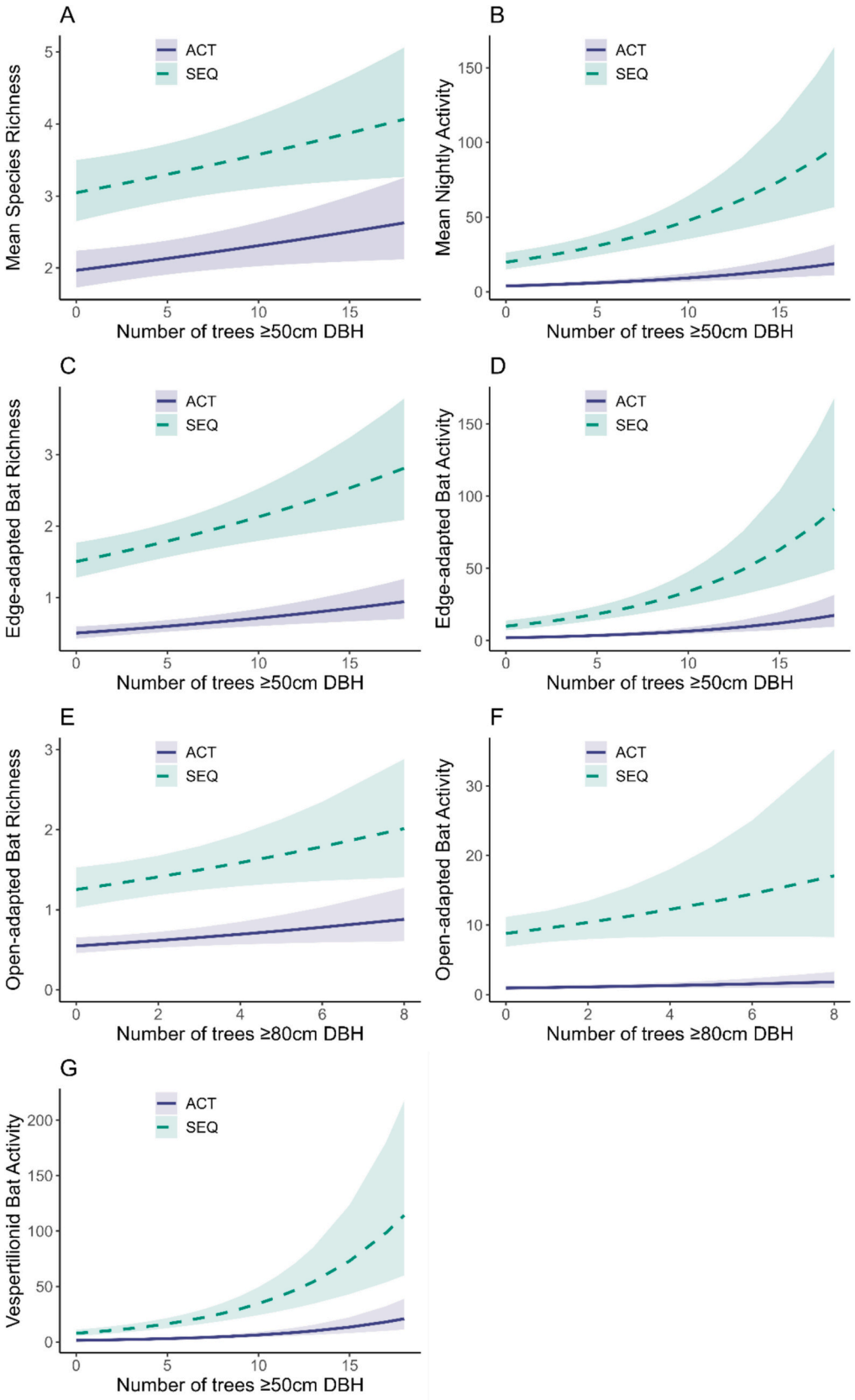

Fig. 1. Predicted mean (± standard error) per detector night of species richness (A), bat activity (B), edge-adapted bat richness (C), edge-adapted bat activity (D), open-adapted bat richness (E), open-adapted bat activity (F) and vespertilionid bat activity (G) with changes in the number of large trees and region.

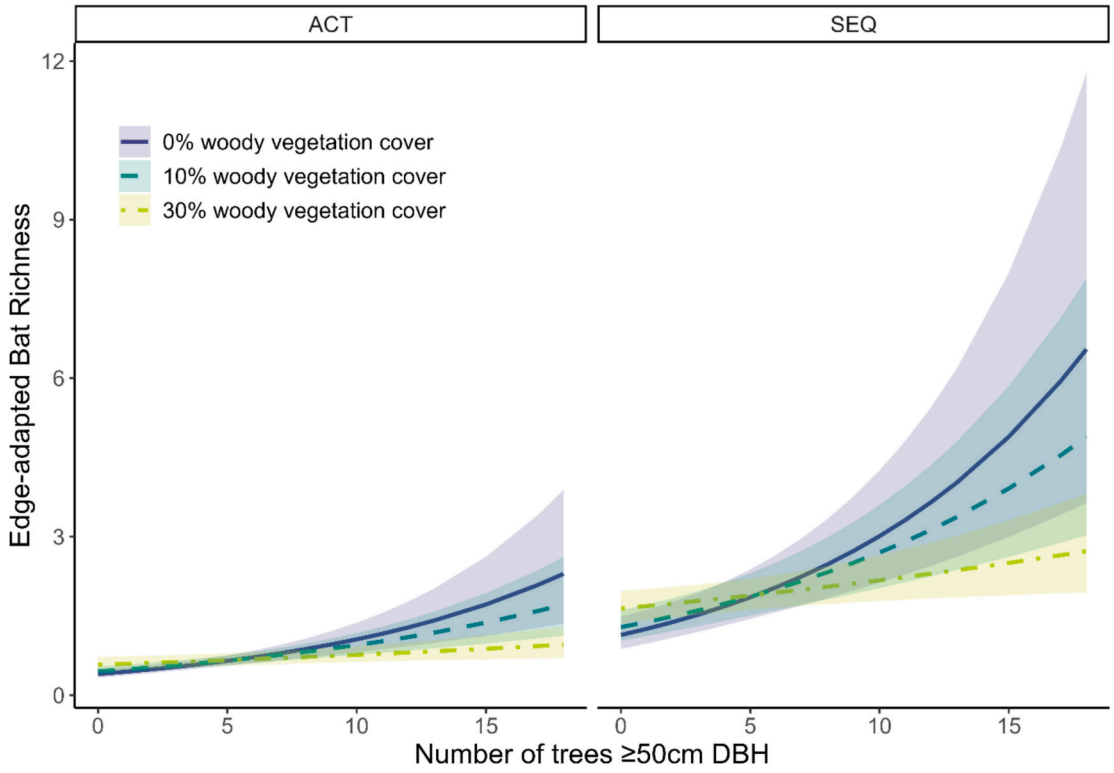

Fig. 2. Predicted nightly mean per detector (± standard error) richness of edge-adapted bats with changes in the number of trees ≥50 cm DBH and woody vegetation cover within 200 m. Woody vegetation cover values (0 %, 10 % and 30 %) represent the 25th, median and 75th percentiles for woody vegetation cover within a 200 m radius of each site.

200 m radius. For activity of open-adapted bats there were only weak positive associations with large trees or with woody vegetation cover. However, for richness of edge-adapted bats, our results indicate that large trees had greater value where they occurred in areas with less total woody vegetation cover. Thus, our results suggest that when large trees are isolated, they hold more importance for edge-adapted insectivorous bats. To the best of our knowledge, this interaction between large trees, surrounding woody vegetation cover and bat community metrics has not been studied directly, outside of Le Roux et al. (2017).

Single isolated trees are known to be centres of activity for bats, and other wildlife, in other landscapes (Law et al., 2000). Large trees offer more value when they are in isolation for birds, with this relationship particularly strong for hollow-dependent species (Le Roux et al., 2017; Parsons et al., 2025; Stagoll et al., 2012). Given that bats tend to hunt near trees, particularly edge-adapted bats, and are likely to have roosts in tree hollows, it follows that their relationship with large trees in the urban context could mirror that of birds. When large trees are in isolation, their value is concentrated, compared with a more diluted value when situated within a patch of vegetation. That is, the richness of edge-adapted and of open-adapted bats were predicted to be higher at isolated trees, as the bats are drawn to those trees as pillars in the landscape. When the large trees were a part of a more vegetated landscape, the richness of bats to be associated with individual trees was less as the bats would be more dispersed.

While our data may show that open-adapted bats are less likely to be associated with large trees or woody vegetation cover, this is likely related to their detectability. Given their flight style and hunting technique, these bats fly over open spaces and long distances, thus reducing the likelihood of these bats being recorded within proximity to trees. However, all the open-adapted bat species we identified utilise tree hollows as roosting spaces (Churchill, 2008; McConville and Law, 2013; Rhodes and Wardell-Johnson, 2006). Therefore, despite our data not indicating strong evidence of associations between activity of open-adapted bats and large trees, large trees are still important for their conservation.

4.3. Urban bat community

Variation between regions results in part from differing endemicity of bat species, in connection with climate and habitat differences. To determine what proportion of geographically available insectivorous bat species were present we used the Australasian Bat Society (2023) BatMap, searching for all families of suborder Vespertilioniformes or Yangochiroptera within 150 km of the centre points for each of our study regions (Milne et al., 2023). There are 21 extant species of microbat in the ACT, and 28 extant species in SEQ. The ACT urban matrix is a temperate landscape with cooler average temperatures, more scattered trees, and lower overall woody vegetation cover. SEQ supports a higher richness of bat species. The SEQ region is subtropical with higher humidity and average rainfall, as well as more woody vegetation cover. Presuming that both species were present from each species complex, we recorded evidence of 62 % of all potentially present microbats in the ACT, and 64 % in SEQ.

Given the high numbers of calls recorded in urban environments, we were also able to evaluate the sensitivity of the recorded bat species to urbanisation (Table 2). Having an indication of the sensitivity to urbanisation expressed by these species will help to inform future conservation planning. Threlfall et al. (2012) provided initial urban sensitivity ratings for 17 bat species (and the *Nyctophilus* spp. complex) found in Sydney, Australia. Eleven of the species/species complexes overlapped with those recorded in our study, including representation of species that are very sensitive, moderately sensitive and tolerant to urban areas. Our recording of a further minimum six species indicates that more insectivorous bats may be utilising urban areas than previously thought. For example, we recorded *Chalinolobus nigrogriseus*, *Scotorepens* species complex and *Ozimops planiceps* each at a minimum of 70

% of the sites in their applicable regions, with total call counts at a minimum of 600.

Interestingly, Wolf et al. (2022) developed a methodology to determine an 'urban affinity' value for 50 insectivorous bat species globally. They assigned an urban affinity value for nine of the same species we recorded, however, their ratings do vary from the results we have observed. For example, they reported that *C. gouldii* had a mean urban affinity ranking of 27, thus midway on the scale. *C. gouldii* is regularly reported as a highly prevalent bat in urban areas in Australia, including the present study (Godinho et al., 2020; Griffiths et al., 2017; Threlfall et al., 2011). While urban affinity ratings of this type are valuable, they should be considered indicative only.

While some of the variation between different bat metrics can be explained by bat morphology and hunting technique, there is also evidence that some species are more sensitive to urbanisation in other ways. Li and Wilkins (2022) reported that small bats responded positively to spatially cluttered urban sites, whereas open-adapted bats preferred open sites lacking the spatial clutter of built structures. Le Roux et al. (2017) reported two bats in his ACT study were only recorded in nature reserves, *S. flaviventris* (open-adapted) and *F. tasmaniensis* (edge-adapted). While we recorded high activity of *M. norfolkensis* in urban greenspace in SEQ, prior research in New South Wales, Australia found that this species preferred low-lying, non-urban riparian areas (McConville et al., 2014). Additionally, we do acknowledge the limitations in our data by only sampling for one season, and for different months per region. Future research would be recommended to sample across multiple seasons to account for variability in bat activity (Gonsalves and Law, 2018).

4.4. Implications for residential development

The protection of large trees in new urban developments focuses on retaining trees within blocks of remnant vegetation rather than as scattered individual trees (Parsons et al., 2023; Phelan et al., 2019; Wintle et al., 2019). In a review of urban forest strategies, Phelan et al. (2019) noted that while land-use planning policies and regulations rarely focused on trees specifically, they still impacted urban forest on private land through the regulation of dwelling density and setting tree planting requirements. Conversely, Rosa et al. (2012) analysed the change in conservation policies by the Brazilian government and reported that while they were effective in reducing the frequency of large scale clearing, smaller clearings by both small and large landholders persisted. While conserving remnant vegetation is critical, the protection of small vegetation patches and scattered trees is highly valuable and should not be discounted in land management practices, particularly in urban environments (Soanes et al., 2019; Wintle et al., 2019).

Our results highlight the importance of tree retention in urban greenspace for bat diversity. The presence of large trees $\geq$50 cm DBH, particularly those in areas with few other large trees, offer valuable habitat that supports a varied community of insectivorous bats. Other works have investigated adjacent relationships among bats and urban green space. Oprea et al. (2009) reported that bat richness, activity and diversity is higher in urban parks than streets without trees, with wooded streets still more similar to non-wooded streets than urban parks. The findings of Moretto et al. (2019) suggest that the effect of adding or removing urban trees influences bats up to 0.25 km away. These findings, in combination with our results, cement the importance of retaining trees as part of a matrix of greenspace interspersed with urban development.

Tree retention in residential developments needs to be prioritised. Most urban forest strategies in Australia currently place heavy focus on planting more street trees without addressing the loss of large trees. There is an insurmountable time lag between trees being planted and reaching the age of maturity to develop hollows, approximately 120–220 years (Gibbons and Lindenmayer, 2002). Additionally, the common solution to replacing or offsetting large trees is nest boxes, and they only offer limited effectiveness (Griffiths et al., 2017; Griffiths et al., 2020; Smith and Agnew, 2002). Our findings support the suggestion that isolated large trees act as keystone structures in urban areas and thus require protection (Le Roux et al., 2015; Parsons et al., 2025; Stagoll et al., 2012). New residential developments can facilitate the retention of isolated large trees by planning more greenspace or creating 'safe space' around large trees to minimise risk, rather than simply opting for tree removal and replacement with seedlings.

CRediT authorship contribution statement

Cara R. Parsons: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Maldwyn J. Evans:** Writing – review & editing, Validation, Methodology, Formal analysis. **Darren S. Le Roux:** Writing – review & editing, Validation. **Saul A. Cunningham:** Writing – review & editing, Validation. **Brad Law:** Writing – review & editing, Validation, Software. **Philip Gibbons:** Writing – review & editing, Validation, Methodology, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Cara Parsons reports financial support was provided by Ecological Society of Australia Ltd. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111146.

Data availability

Data will be made available on request.

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