BIODIVERSITY RESEARCH

The value of scattered trees for wildlife: Contrasting effects of landscape context and tree size

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Funding information
Land Development Agency, ACT Government; Australian Research Council, Grant/Award Number: FT100100358; Fenner School of Environment and Society, Australian National University

Editor: Alan Andersen

Abstract

Aim: The biodiversity value of scattered trees in modified landscapes is often overlooked in planning and conservation decisions. We conducted a multitaxa study to determine how wildlife abundance, species richness and community composition at individual trees are affected by (1) the landscape context in which trees are located; and (2) the size of trees.

Location: Canberra, south-eastern Australia.

Methods: Trunk arthropod, bat and bird surveys were undertaken over 3 years (2012–2014) at 72 trees of three sizes (small (20–50 cm DBH), medium (51–80 cm), large (≥80 cm)) located in four landscape contexts (reserves, pasture, urban parklands, urban built-up areas).

Results: Landscape context affected all taxa surveyed. Trunk arthropod communities differed between trees in urban built-up areas and reserves. Bat activity and richness were significantly reduced at trees in urban built-up areas suggesting that echolocating bats may be disturbed by high levels of urbanization. Bird abundance and richness were highest at trees located in modified landscapes, highlighting the value of scattered trees for birds. Bird communities also differed between non-urban and urban trees. Tree size had a significant effect on birds but did not affect trunk arthropods and bats. Large trees supported higher bird abundance, richness and more unique species compared to medium and small trees.

Main conclusions: Scattered trees support a diversity of wildlife. However, landscape context and tree size affected wildlife in contrasting ways. Land management strategies are needed to collectively account for responses exhibited by multiple taxa at varying spatial scales. We recommend that the retention and perpetuation of scattered trees in modified landscapes should be prioritized, hereby providing crucial habitat benefits to a multitude of taxa.

KEYWORDS
arthropods, bats, birds, conservation planning, human-modified landscapes, large old trees

1 | INTRODUCTION

Landscape modification is one of the biggest global threats to terrestrial biodiversity (Maxwell, Fuller, Brooks, & Watson, 2016; Phalan, Green, & Balmford, 2014). Half of the Earth's terrestrial surface has been impacted by human activity, and by 2050, a further 2–10 million km^2 of remnant vegetation is predicted to be converted for human purposes (Millenium Ecosystem Assessment,

2005; Vitousek, Mooney, Lubchenco, & Melillo, 1997). Human-altered landscapes not specifically devoted to nature conservation can still provide important habitat opportunities for species, but managing these landscapes for biodiversity conservation presents unique challenges (Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013; Lindenmayer et al., 2008; McKinney, 2006). How modified landscapes are managed will ultimately determine the fate of myriad species worldwide and affect the functioning of entire ecosystems (Flynn et al., 2009; Seto, Güneralp, & Hutyra, 2012).

The "habitat fragmentation model" of biodiversity conservation, underpinned by the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), has been a benchmark of conservation science (Warren et al., 2014). However, it is widely recognized that when applied to non-insular, human-modified landscapes, species responses often defy predictions prescribed by island biogeography theory (i.e., habitat isolation and species–area relationships; Ricketts, 2001; Fischer & Lindenmayer, 2002c; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014). Many species do not perceive fragmented landscapes as simple binary units of "habitat" versus "non-habitat" (Didham, Kapos, & Ewers, 2012; Franklin & Lindenmayer, 2009). Alternative conceptual frameworks, like the "habitat variegation model" (McIntyre & Barrett, 1992) and "continuum model" (Fischer & Lindenmayer, 2006), offer more holistic wildlife-oriented approaches recognizing that (1) different taxa perceive and use resources in altered landscapes in different ways; and (2) there are gradients in habitat heterogeneity and intactness ranging from large habitat patches (e.g., nature reserves) to isolated and small habitat resources (e.g., scattered trees).

Scattered trees (isolated remnant and planted trees; Manning, Fischer, & Lindenmayer, 2006) are prominent features of human-modified landscapes worldwide and have been identified as "keystone ecological structures." Large, old scattered trees, in particular, can provide disproportionate habitat benefits for biota relative to their size and availability (Lindenmayer & Laurance, 2017; Lindenmayer et al., 2013). For example, trees in commercial production forests (Matveinen-Huju, Niemelä, Rita, & O'Hara, 2006; Mazurek & Zielinski, 2004), agricultural landscapes (DeMars, Rosenberg, & Fontaine, 2010; Dunn, 2000) and urban environments (Stagoll, Lindenmayer, Knight, Fischer, & Manning, 2012; Yasuda & Koike, 2009) significantly contribute to wildlife diversity. Locally, scattered trees provide distinct microclimates and unique structural elements like hollows and woody debris (Manning, Gibbons, Fischer, Oliver, & Lindenmayer, 2012; Tews et al., 2004). At a landscape scale, scattered trees increase spatial heterogeneity and connectivity that can aid species dispersal (Fischer & Lindenmayer, 2002b; Manning, Gibbons, & Lindenmayer, 2009). Despite growing empirical evidence demonstrating the ecological importance of scattered trees, few studies have quantified response patterns for multiple taxa at individual trees and evaluated whether the use of trees differs between intact and modified landscapes. This knowledge is important as it could help justify tree protection efforts, particularly in modified landscapes.

Scattered trees often lack formal protection and are regularly overlooked in strategic land planning and conservation priorities (Hartel et al., 2013; Plieninger et al., 2015; Stagoll et al., 2012). Tree retention in modified landscapes can be a highly contentious issue that conflicts with human interests and activities including logging (Laurance, Delamonica, Laurance, Vasconcelos, & Lovejoy, 2000), wood production (Lutz, van Wagtendonk, & Franklin, 2009), crop cultivation (Gibbons, Lindenmayer, & Fischer, 2008), livestock grazing (Fischer, Zerger, Gibbons, Stott, & Law, 2010), urbanization (Le Roux, Ikin, Lindenmayer, Manning, & Gibbons, 2014) and public safety of residents (Carpaneto, Mazziotta, Coletti, Luiselli, & Audisio, 2010). Many applied management policies and practices remain skewed towards a traditionalist conservation framework governed by the original principles of island biogeography, which advocate that "intact" and "large" are more valuable for biodiversity than "isolated" and "small" (Franklin & Lindenmayer, 2009; Mendenhall et al., 2014). For example, wildlife management plans and biodiversity offset schemes often tend to focus on enhancing or enlarging intact reserves rather than also looking at ways to conserve isolated habitat resources dispersed within disturbed landscapes, which may yield considerable benefits for biodiversity (Cunningham et al., 2014; Mendenhall, Shields-Estrada, Krishnaswami, & Daily, 2016; Moilanen, Van Teeffelen, Ben-Haim, & Ferrier, 2009). An underlying assumption that scattered trees have limited biodiversity value (and aesthetic or economic value) because they are isolated and located in highly degraded or human-dominated landscapes underpins many policies and practices that facilitate intentional tree removal (Gibbons et al., 2009; Le Roux et al., 2014; Manning et al., 2006). Effectively, scattered trees may be "triaged" or sacrificed in favour of the preservation of larger, intact habitat patches (e.g., exemptions allowing paddock tree removal; NSW Government, 2014). But is this land management approach justified, or should scattered trees also be retained in addition to protected areas?

In this study, we aimed to quantify the biodiversity value of scattered trees: (1) located in different landscape contexts; and (2) of different tree sizes. We conducted a multitaxa study at individual trees targeting trunk arthropods, bats and birds. We tested two predictions based on the premise that many real-world conservation and management practices remain largely governed by an overextension of the principles of island biogeography.

Prediction 1 (landscape context): trees located in a more intact semi-natural landscape support greater wildlife abundance, richness and more distinct communities compared with trees located in modified landscapes.

Prediction 2 (tree size): large trees support greater wildlife abundance, richness, and distinct communities compared with medium and small trees.

Our study has important implications for tree management and biodiversity conservation. To our collective knowledge, this is one of the first studies to explicitly test the effects of both landscape context and tree size on a wide range of taxa.

2 | METHODS

2.1 | Study area

We conducted our study in the Australian Capital Territory (ACT), south-eastern Australia (35°17′35.64″S; 149°07′27.36″E). The study area occupies 814 km² and supports a population of approximately 410,000 people (Australian Bureau of Statistics, 2017). Native temperate woodlands once dominated the region and are characterized by two tree species, yellow box (*Eucalyptus melliodora*) and Blakely's red gum (*Eucalyptus blakelyi*). Tree clearance for farming and urban development has led to an approximately 95% decline in woodland habitat in the region, which is listed as a critically endangered ecological community (Department of the Environment, 2015).

2.2 | Study design

We stratified our study area into four dominant landscape contexts: (1) reserves (semi-natural conservation areas); (2) pasture (grazed agricultural land); (3) urban parklands (public greenspace ≥ 0.2 ha); and (4) urban built-up areas (public greenspace < 0.2 ha located in residential areas (e.g., roadside margins; Figure 1)). In each landscape context, we randomly sampled six small trees (20–50 cm diameter at breast height (DBH)), six medium trees (51–80 cm DBH) and six large trees (>80 cm DBH). This resulted in 12 treatment combinations and 72 sample trees (Tables S1–S4). We selected sample trees that were spaced at least 250 m apart (mean spacing (m) = 917.97 ± 91.36) to minimize spatial dependence. Mantel tests confirmed no spatial autocorrelation occurred between sample trees for wildlife responses (*r* = −.002 to .05; *p*-value < .05). Sample trees were located across nine reserves, four rural landholdings, 18 urban parklands and 18 urban built-up areas, which collectively spanned approximately 50 km². We restricted sample trees to native *Eucalyptus* species grouped as "yellow box" (*n* = 24), "Blakely's red gum" (*n* = 24) and "other eucalypt species" (*n* = 24). The DBH, height and canopy width of sample trees in each tree size category did not differ significantly across landscape contexts (*H* = 0.8–6.8, *p* < .05, Kruskal–Wallis ANOVAs).

2.3 | Wildlife surveys

We conducted wildlife surveys at all 72 sample trees during spring (September–November) over three consecutive years (2012–14), avoiding surveying during unfavourable weather.

FIGURE 1 Map of study area showing the sampling design across different landscape contexts and tree sizes in Canberra, Australia. Examples of large (>80 cm DBH) trees located in different landscape contexts are also shown, including (a) semi-natural reserves, (b) grazed pasture, (c) urban parklands and (d) urban built-up areas. [Colour figure can be viewed at wileyonlinelibrary.com]

2.3.1 | Trunk arthropods

In each year, we used two survey techniques to capture trunk arthropods. First, we used one glue trap (20 × 10 cm; STV International Ltd, UK) secured to the trunk of each tree at a height of 1.5 m for one night. Second, we conducted a five minute active search at each tree, which involved looking under peeling bark (minimizing stripping of bark where possible) and inspecting the tree trunk within a standardized area (30 cm wide × 2 m aboveground). Each survey method was undertaken on a different day at each tree, but not all trees were surveyed on the same day. We sorted arthropods into orders and morphospecies (following Zborowski & Storey, 2010).

2.3.2 | Bats

In each year, we recorded bat activity using Anabat detectors (Titley Scientific, Australia). We secured a single bat detector to the trunk of each tree at a height of 2 m, and all echolocation passes (two or more pulses) were recorded between sunset and sunrise during one night (Threlfall, Law, & Banks, 2012a). We positioned the detector microphone upwards to restrict recording to the tree (approximately 60° from the horizon). Microphones were directional (detection distance and angle of at least 20 m and 60°, respectively). We also conducted ultraviolet (UV) light trap surveys on a separate night in each year between sunset and sunrise to account for arthropod abundance in the vicinity of each tree. We secured one UV trap (Australian Entomological Supplies, Australia) to the trunk of each tree at a height of 1.5 m. We processed echolocation passes using AnalookW and Anascheme software (M. Gibson, Ballarat University, unpublished) and a regional call identification key (Adams, Law, & Gibson, 2010). Calls from two sympatric long-eared bat species were indistinguishable and classified as a species complex (*Nyctophilus* sp.). It was not possible to obtain abundance data from acoustic recordings, and we instead used relative bat activity (passes/tree/night). Bat and arthropod surveys were not undertaken on the same night at each tree.

2.3.3 | Birds

In each year, we conducted two separate visual fixed point bird surveys at each tree. Each survey was 20 min in duration (Fischer & Lindenmayer, 2002a). Surveys involved sitting 5–10 m from each tree and recording the abundance and identity of species that came into direct contact with each tree. Surveys were conducted during the breeding period (September and October) when individuals exhibit strong site fidelity (Recher, Kavanagh, Shields, & Lind, 1991).

2.4 | Statistical analyses

2.4.1 | Abundance and richness

We used generalized linear mixed models (GLMM) to predict variation in trunk arthropod abundance and morphospecies richness, bat activity and richness, and bird abundance and richness and to identify the relative effect of explanatory variables. We fitted "landscape context," "tree size," "year" and "tree species" as fixed effects. We fitted "tree identity" as a random effect to account for repeat surveys across years and at sample trees. For bat models only, we also tested the fixed effect of "arthropod abundance from UV captures per tree." Arthropod abundance was not fitted as a covariate for bird models as not all bird species were insectivorous. For trunk arthropods and birds, we also investigated fixed effects for different orders and functional guilds, respectively. Only trunk arthropod orders that were present at >10% of trees over the three-year survey period were considered (Arachnida, Coleoptera, Diptera, Hymenoptera, Hemiptera and Lepidoptera). For birds, species of conservation concern in our study region (Rayner, Lindenmayer, Wood, Gibbons, & Manning, 2014; Rayner et al., 2015) and dominant guilds were considered (small insectivore, hollow nester). We fitted normal distributions (identity link) to log-transformed abundance data and Poisson distributions (log link) to richness data. Chi-squared tests were used to compare interaction (landscape context × tree size) and additive (landscape context + tree size) models. A significant interaction term was recorded only for bird abundance (likely attributed to small sample sizes of only six trees per interaction term), while all others results were reported only for additive models. The significance of each term was checked by comparing the full model to the model without that term.

2.4.2 | Community composition

We used generalized permutational multivariate analyses of variance (PERMANOVA) to examine variation in trunk arthropod order, bat species and bird species composition (Anderson & Robinson, 2003). We fitted "landscape context" and "tree size" in a two-way fixed-factor design. We then conducted a separate analysis using constrained canonical analyses of principal coordinates using discriminant analysis (CAP (CDA)), which finds axes maximizing separation among groups (Anderson & Willis, 2003). Constrained ordination is useful to examine compositional data against set predictions; in our case, as defined *a priori* by landscape context (prediction 1) and tree size (prediction 2). Correlations between taxa and canonical axes were used to identify taxa that contributed strongly to community distinctiveness (correlations > (±) 0.2). For multivariate analyses, we used a Bray–Curtis dissimilarity index on square root-transformed abundance data (and bat activity data) pooled across survey years with 10,000 permutations.

3 | RESULTS

We recorded a total of 7,776 trunk arthropods identified to 15 orders; 30,536 bat echolocation passes assigned to 11 species; and 1,785 birds identified to 61 species (see Table S5 for recorded taxa).

3.1 | Effect of landscape context

Landscape context had a significant effect on all taxa surveyed, but response patterns were highly variable among taxa.

TABLE 1 Summary of main effects (*p*-values, bolded) for generalized linear mixed models (GLMM; abundance (or activity) and richness data) and permutational multivariate analyses of variance (PERMANOVA; assemblage data) for trunk arthropods, bats and birds (see also Tables S6 and S7)

Response	Fixed effects					
	Landscape context	Tree size	Landscape context * tree size	Tree species	Year	Log (arthropod abundance UV captures/tree)
Trunk arthropod						
Abundance	0.350	0.147	—	0.355	**0.002**	—
Richness (morphospecies)	0.738	0.695	—	0.556	**<0.001**	—
Assemblage (orders)	**0.032**	0.644	—	—	—	—
Bat						
Activity	**<0.001**	0.834	—	0.750	**<0.001**	**<0.001**
Richness	**<0.001**	0.749	—	0.966	0.504	**0.040**
Assemblage	**<0.001**	0.782	—	—	—	—
Bird						
Abundance	—	—	**0.044**	**0.004**	0.830	—
Richness	**0.027**	**<0.001**	—	**0.013**	0.557	—
Assemblage	**<0.001**	**<0.001**	—	—	—	—

3.1.1 | Trunk arthropods

We found that landscape context had no significant effect on trunk arthropod abundance and morphospecies richness (Table 1; Figure 2a and b). However, analyses on dominant trunk arthropod orders revealed significant variation in Diptera (flies) abundance (*p* = .021), Diptera morphospecies richness (*p* = <.001) and Arachnida (spiders) morphospecies richness (*p* = .022) across landscape contexts (Table 2; see Tables S6 and S7 for statistical summaries). For flies, we found greater abundance and morphospecies richness at trees in reserves, compared to trees in modified landscapes. For spiders, greater morphospecies richness was recorded at trees in modified landscapes compared to trees in reserves. Further, landscape context had a significant effect (*p* = .032) on arthropod community composition (Figure 3a). There was a significant pairwise difference (*p* = .016) between trunk arthropod communities recorded at trees in urban built-up areas and reserves. Urban built-up areas were characterized by communities with high abundance of Hymenoptera (ants). Reserve communities were characterized by high abundance of Diptera (flies), Coleoptera (beetles) and Arachnida (spiders).

3.1.2 | Bats

We found that landscape context had a significant effect (*p* < .001) on bat activity and richness (Table 1). At trees in urban built-up areas, bat activity and richness were significantly reduced compared with urban parklands, pasture and reserves (Figure 2c and d). Landscape context also had a significant effect (*p* < .001) on bat community composition (Figure 3b). There were significant pairwise differences (*p* < .001) between bat communities recorded at trees in urban built-up areas and

all other landscape contexts, with urban built-up communities characterized by low levels of bat activity for all species. Two bat species were recorded only in reserves (eastern false pipistrelle (*Falsistrellus tasmaniensis*) and yellow-bellied sheath-tailed bat (*Saccolaimus flaviventris*)).

3.1.3 | Birds

We found that landscape context had a significant effect on bird richness (*p* = .027; Table 1). More species were recorded at trees in pasture, urban parklands and urban built-up areas compared with trees in reserves (Figure 2e and f). Analyses of dominant bird guilds revealed that more individuals (*p* = .024) and bird species (*p* = .008) of conservation concern were recorded at trees in some modified landscapes (pasture and urban parklands) compared to reserves (Table 2). Landscape context also had a significant effect (*p* < .001) on bird community composition (Figure 3c). There were significant pairwise differences (*p* < .001) between bird communities recorded at non-urban trees (reserves and pasture) and urban trees (parklands and built-up areas). Communities at urban trees were characterized by high abundance of urban-adapted native species (e.g., Australian magpie (*Cracticus tibicen*)) while non-urban trees were characterized by high abundance of hollow-nesting species (e.g., crimson rosella (*Platycercus elegans*)). Some species were recorded only in reserves (e.g., brown thornbill (*Acanthiza pusilla*)).

3.2 | Effect of tree size

Tree size had a significant effect on birds but did not affect trunk arthropods and bats.

(a) Trunk arthropod abundance

(b) Trunk arthropod richness

(c) Bat activity

(d) Bat richness

(e) Bird abundance
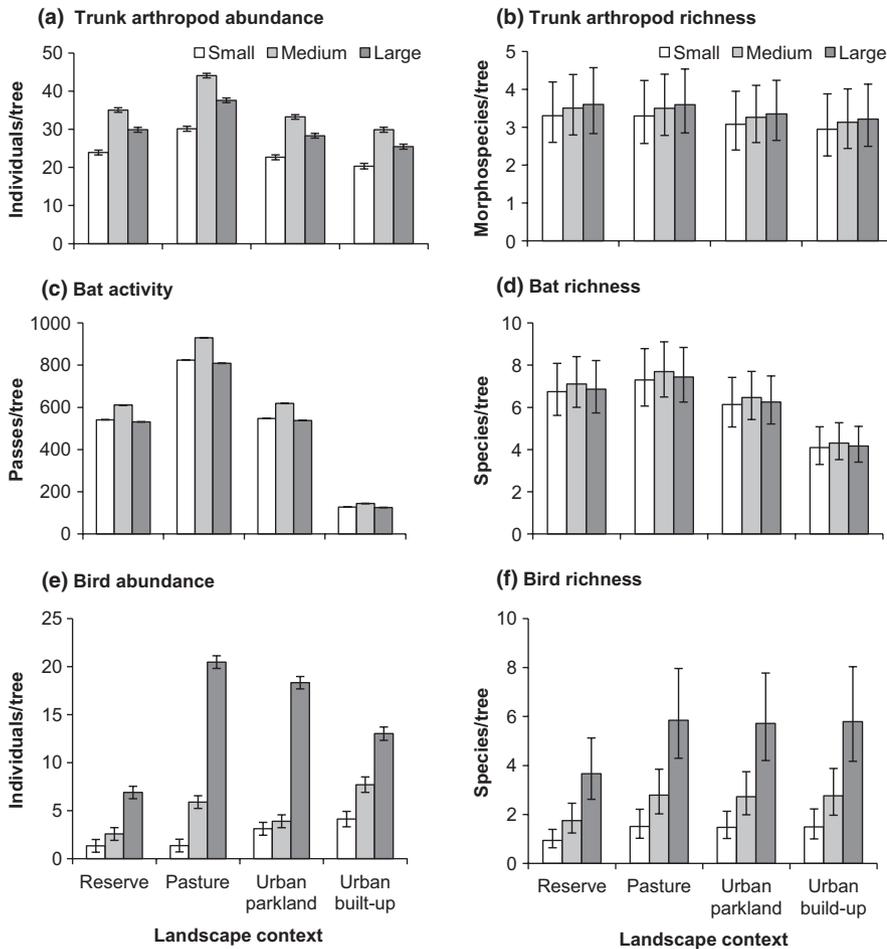
(f) Bird richness

FIGURE 2 Predicted patterns of variation (means ± SEM) derived from generalized linear mixed models (GLMM) showing wildlife abundance and richness across different landscape contexts and tree sizes. Measures of wildlife responses include (a) trunk arthropod abundance, (b) trunk arthropod morphospecies richness, (c) relative bat activity (diminutive SEM), (d) bat species richness, (e) bird abundance and (f) bird species richness

3.2.1 | Trunk arthropods

We found no significant effect of tree size on trunk arthropod abundance, morphospecies richness or community composition (Table 1). We also found no significant effect of tree species on trunk arthropod abundance and morphospecies richness. However, analyses on dominant trunk arthropod orders revealed significant variation in Arachnida (spiders) abundance ($p = .019$) across tree sizes, with large and medium trees tending to support more spiders than small trees.

3.2.2 | Bats

We found no significant effect of tree size on bat activity, richness or community composition (Table 1). We also found no significant effect of tree species on bat activity and richness. However, arthropod abundance at trees had a significant positive effect on bat activity ($p < .001$) and richness ($p = .040$).

3.2.3 | Birds

We found a significant ($p = .044$) interaction between landscape context and tree size for bird abundance but not for bird richness. Large trees in modified landscapes supported the highest abundance of birds (Figure 2e and f). Tree size had a significant effect on bird

richness ($p < .001$; Table 1). More species were recorded at large trees compared with medium trees and small trees. We also recorded significantly ($p < .001$) more individuals and species of small insectivores, hollow nesters and species of conservation concern at large trees (Table 2). Tree species had a significant effect on bird abundance ($p = .004$) and richness ($p = .013$). Overall, more individuals and species were recorded at Blakely's red gum and at "other eucalypt" species compared to yellow box.

We found that tree size also had a significant effect ($p < .001$) on bird community composition (Figure 3d). There were significant pairwise differences between bird communities recorded at large trees and medium trees ($p = .026$) and large trees and small trees ($p < .001$). The bird community at large trees represented a diversity of functional guilds, including hollow nesters (e.g., galah (*Cacatua roseicapilla*)), nectarivores (e.g., yellow-faced honeyeater (*Lichenostomus chysops*)), aerial insectivores (e.g., willie wagtail (*Rhipidura leucophrys*)), habitat generalists (e.g., magpie lark (*Grallina cyanoleuca*)), urban-adapted native species (e.g., red wattlebird (*Anthochaera carunculata*) and exotic species (e.g., common myna (*Acridotheres tristis*)). Approximately a quarter (26.2%) of bird species (16 unique species) were recorded only at large trees compared to 11.5% (seven unique species) at medium trees and 3.3% (two unique species) at small trees. Some guilds were exclusively recorded at large trees, including raptors (e.g., brown falcon (*Falco berigora*)) and threatened species (e.g., superb parrot (*Polytelis swainsonii*); Table S5).

TABLE 2 Summary of main effects (*p*-values, bolded) for generalized linear mixed models (GLMM; abundance and morphospecies richness data) for trunk arthropod orders found at >10% of trees over the three-year study period and dominant bird guilds, including species of conservation concern (see also Table S6)

Response	Fixed effects			
	Landscape context	Tree size	Tree species	Year
Trunk arthropod				
Coleoptera abundance	0.799	0.391		0.496
Coleoptera richness	0.963	0.442		0.643
Diptera abundance	**0.021**	0.530		0.303
Diptera richness	**<0.001**	0.211		0.176
Hymenoptera abundance	0.677	0.494		0.197
Hymenoptera richness	0.404	0.293		0.305
Lepidoptera abundance	0.141	0.948		0.233
Lepidoptera richness	0.121	0.743		0.492
Arachnida abundance	0.145	**0.019**		0.354
Arachnida richness	**0.022**	0.146		0.314
Hemiptera abundance	0.249	0.741		0.763
Hemiptera richness	0.269	0.714		0.626
Bird				
Conservation concern abundance	**0.024**	**<0.001**	0.273	0.090
Conservation concern richness	**0.008**	**<0.001**	0.405	0.180
Small insectivore abundance	0.075	**<0.001**	**<0.001**	0.536
Small insectivore richness	0.050	**<0.001**	**<0.001**	0.175
Hollow-nester abundance	0.178	**<0.001**	0.134	0.869
Hollow-nester richness	0.136	**<0.001**	0.293	0.610

4 | DISCUSSION

We tested two predictions examining how wildlife is affected by (1) the landscape context in which trees are located; and (2) the size of trees. Landscape context had a significant effect on all taxa surveyed. Responses by trunk arthropods, bats and birds deviated from our "landscape context" prediction, which anticipated that the highest abundance, richness and most distinct wildlife communities would occur at trees located in relatively intact landscapes (reserves). Instead, wildlife exhibited more complex responses, underscoring the important biodiversity value of scattered trees situated in modified landscapes (see Figure 4a for a conceptual model). Tree size had a significant effect on birds but did not affect arthropods and bats. For birds only, this response was consistent with our "tree size" prediction (Figure 4b), which predicted that the greatest wildlife diversity would occur at large trees. However, trees of all sizes were important for trunk arthropods and bats.
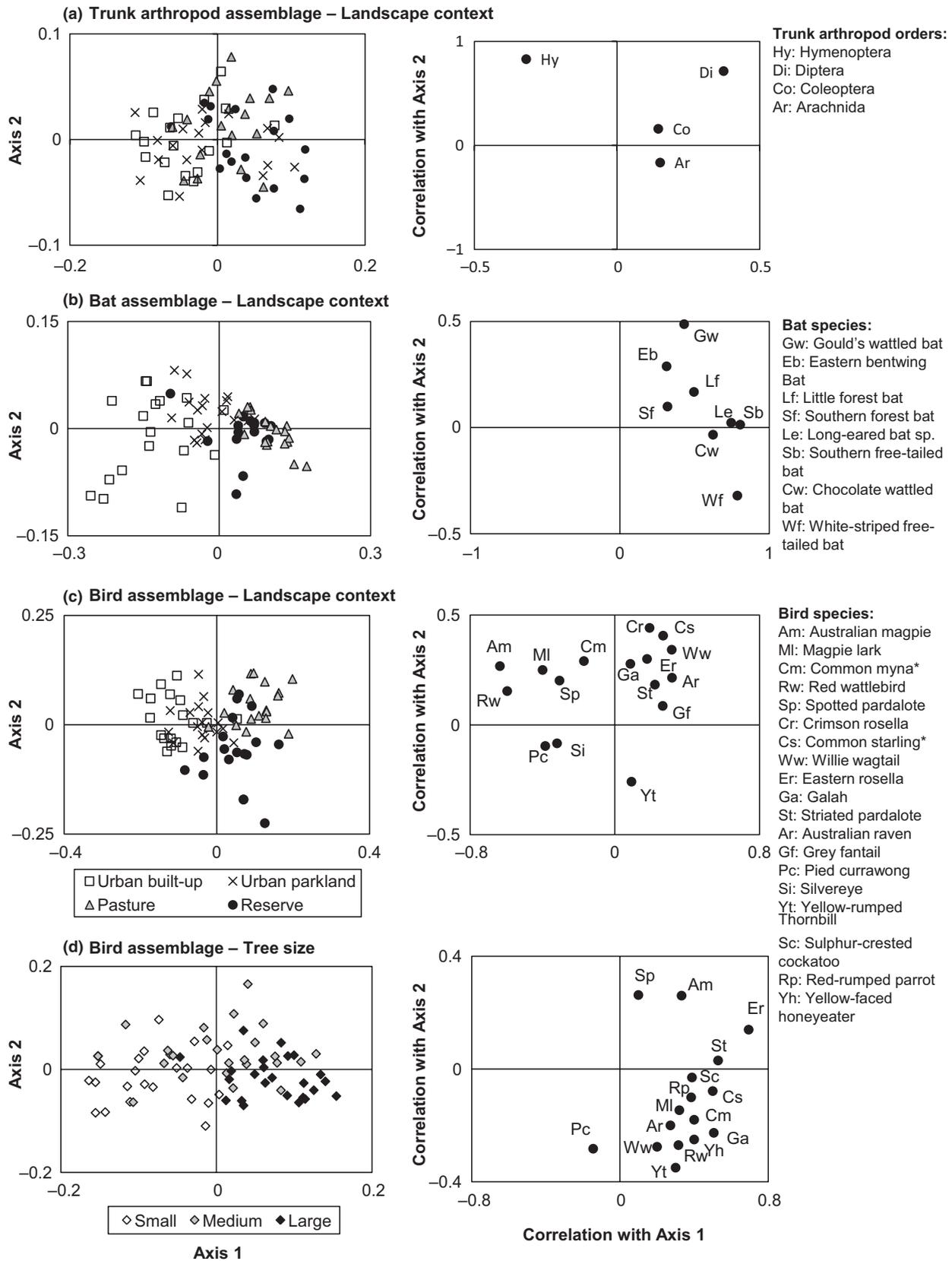
4.1 | Effect of landscape context

We found that trees in modified landscapes supported similar trunk arthropod abundance and morphospecies richness as trees in reserves (Table 1; Figure 2a and b). This result highlights that, even in modified environments, trunk arthropod populations can still be diverse

and abundant at scattered trees (Figure 4a). Trunk arthropods are also likely to be important prey items for higher order animals such as birds and bats (Bhullar & Majer, 2000; Ostfeld & Keesing, 2000).

We found a significant difference between arthropod communities at trees in urban built-up areas and reserves. Trees in urban built-up areas supported high abundance of Hymenoptera (ants; Figure 3a), a result consistent with the findings of Yasuda and Koike (2009), which found diverse ant communities using trunk microhabitats at scattered urban trees. It is possible that ant communities recorded at trees in urban built-up areas are dominated by generalist species capable of exploiting patchy resources; however, more detailed assemblage data are needed to verify this (see also Bang & Faeth, 2011; Menke et al., 2011). Trees in reserves supported high abundance of Diptera (flies), Coleoptera (beetles) and Arachnida (spiders), which constitutes a wide variety of arthropod biota and may include more specialist groups (e.g., predators and parasites) sensitive to the availability of resources readily available in reserves (e.g., carrion; Barton, Cunningham, Lindenmayer, & Manning, 2013). Conserving trees of different sizes across a variety of land use types will likely benefit a wide range of arthropod communities.

Landscape context had a significant effect on small, insectivorous echolocating bats. At trees in urban built-up areas, bat activity and richness were significantly reduced compared to trees in urban parklands, pasture and reserves (Figure 2c and d). Even for Gould's

FIGURE 3 Patterns of variation in wildlife community composition based on significant landscape context and tree size effects. Biplots show (left panels) constrained multivariate canonical analyses of principal coordinates using discriminant analysis (CAP (CAD)), and (right panels) corresponding correlations between canonical axes with taxa driving compositional distinctiveness. Wildlife assemblages include (a) trunk arthropod orders (landscape context effect), (b) bat species (landscape context effect) and (c and d) bird species (landscape context and tree size effects). Introduced bird species are denoted with an asterisk

wattled bat (*Chalinolobus gouldii*), a species considered tolerant of urban development (Threlfall et al., 2012a), we recorded 45%–63% fewer echolocation passes at trees in urban built-up areas compared to trees in other landscape contexts. For long-eared bats (*Nyctophilus gouldi* and *Nyctophilus geoffroyi*), species considered more sensitive to urbanization, activity was reduced by 85%–96% at trees in urban built-up areas. This trend was consistent for all bat species (Figure 3b). These results suggest that anthropogenic factors in built-up urban areas may disturb insectivorous bats. Some bat species may be sensitive to artificial light (Threlfall, Law, & Banks, 2013) and traffic noise (Le Roux & Waas, 2012), while high densities of structures like roads may pose barriers that restrict bat movement (Berthinussen & Altringham, 2012). Our results suggest that bats have a high dependence on trees retained in urban greenspace (parklands) and non-urban habitats (reserves and pasture) where fewer anthropogenic disturbances occur (e.g., street lights; Hale, Fairbrass, Matthews, Davies, & Sadler, 2015). Further investigations into foraging and roosting behaviour could better identify how trees in different landscape contexts are used by insectivorous bats.

Landscape context had a significant effect on birds. Scattered trees in pasture, urban parklands and urban built-up areas supported significantly more birds and bird species than trees in reserves (Figures 2e,f and 4a). One explanation for this response may be related to tree availability across landscape contexts in our study area (see Table S1). That is, scattered trees may have a higher marginal value inversely proportional to their availability in the landscape, consistent with a "diminishing returns" model (Cunningham et al., 2014). It is possible, that in a nature reserve setting, the probability of birds landing at a given tree is less likely because each tree is effectively "diluted" among many trees located in close proximity. This does not mean that aggregated trees in reserves are not important for birds, but rather underscores the exceptional biodiversity importance of isolated trees. Isolated trees have previously been shown to be disproportionately important "lifeboats" for birds in other "hostile" environments (DeMars et al., 2010; Manning, Lindenmayer, & Barry, 2004).

Non-urban and urban trees supported significantly different bird communities (Figure 3c). A high abundance of common hollow-nesting species (e.g., crimson rosella) at pasture and reserve trees is likely related to a higher availability of hollows in these landscapes compared to urban environments, where hollow-bearing trees may be reduced (Le Roux, Ikin, Lindenmayer, Blanchard et al., 2014). However, urban trees supported a high abundance of urban-adapted native species (e.g., Australian magpie), which typically exploit resources in urban areas. Compositional distinctiveness across urban-reserve gradients is thus likely attributed to variation in habitat structure and species tolerance to urbanization (Ikin et al., 2014; Rayner et al., 2015).

4.2 | Effect of tree size

We found that tree size had a significant effect only on birds (Table 1). In all landscape contexts, large trees supported significantly more

individuals and bird species (including small insectivores, hollow nesters and species of conservation concern; Table 2) compared with medium and small trees. However, this response was pronounced at large trees located in modified environments (Figures 2e,f and 4b). These findings suggest that the unique habitat structures associated with large trees are especially attractive for birds in modified environments where resources may be limited (Le Roux, Ikin, Lindenmayer, Manning, & Gibbons, 2015; Manning et al., 2012). Large scattered trees support complex canopies with dead and living branches important for perching; hollows that are crucial nesting resources; and large quantities of decorticating bark, flowers and nectar that are important foraging resources (Dean, Milton, & Jeltsch, 1999; Fischer, Stott, & Law, 2010; Stagoll et al., 2012). Large trees also supported a more unique bird community compared to medium and small trees (Figure 3d). A quarter of all bird species were recorded exclusively at large trees, highlighting that younger, smaller trees alone will not be sufficient to support all bird species.

We did not find a significant tree size effect for bats and trunk arthropods. One plausible explanation for this result may be that birds likely perceive trees in different ways to bats and arthropods. Birds are highly visually orientated and may be more selective of tree-level attributes, particularly structural features associated with larger trees (e.g., canopy attributes, hollow availability; Manning, Lindenmayer, & Barry, 2004). Further, bird responses were related to tree species, but bat responses were related to arthropod abundance (Table 1). In addition, the effect of tree size may not have been detected for bats due to differences in sampling methods. Point count surveys for birds measured direct bird–tree associations, but bat detector surveys were a more indirect sampling approach by comparison. It is also possible that tree size effects for birds may be an artefact of standardized sampling effort across tree sizes (i.e., large trees support more habitat "area," and thus more birds, than smaller trees; but see Le Roux, Ikin, Lindenmayer, Manning et al., 2015).

## 4.3 | Implications for biodiversity conservation

We have demonstrated that scattered trees support a rich variety of trunk arthropod, bat and bird species, including many species of conservation concern. Our results emphasize that there are inconsistencies between traditional predictions associated with island biogeography theory (i.e., that the equilibrium number of species decreases for smaller, isolated patches), which still underpin many management policies. *In situ* animal responses defied simplistic theoretical models (Figure 4). Instead, our results were more consistent with a "habitat variegation" (McIntyre & Barrett, 1992) and "continuum model" (Fischer & Lindenmayer, 2006) of biodiversity conservation. That is, wildlife, especially mobile taxa capable of dispersing beyond reserve boundaries, clearly interacts with the landscape as a heterogeneous "playing field" where habitat opportunities exist in different land use types. This includes exploiting isolated resources like scattered trees.

We argue that there is an urgent need to re-examine land management policies and practices that fail to prioritize the conservation

(a) Landscape context
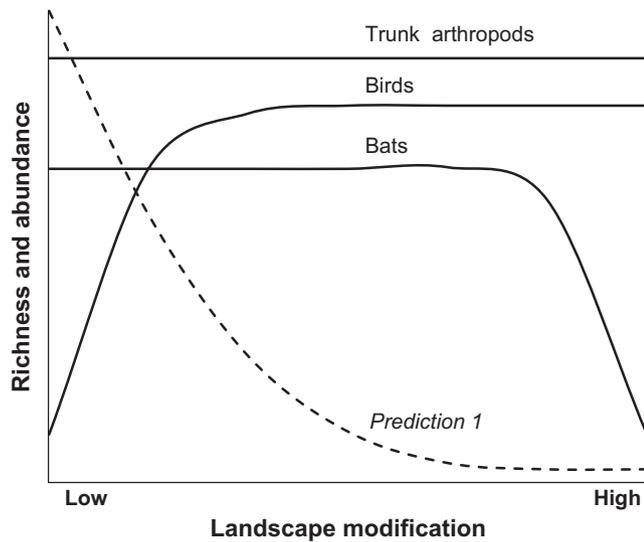
(b) Tree size
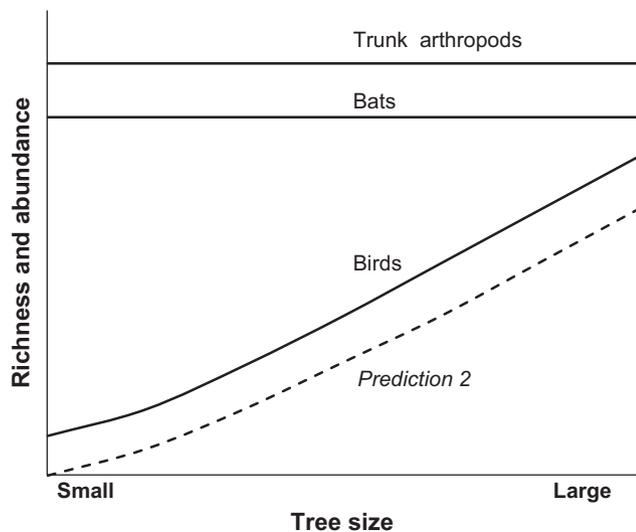
FIGURE 4 Conceptual models illustrating wildlife responses quantified at scattered trees (a) located in different landscape contexts and (b) of different sizes. Wildlife exhibited complex and contrasting responses that often deviated from tested predictions. Predictions were based on the premise that many real-world management practices remain governed by biogeographic principles, resulting in the prioritization of large, intact habitat areas for conservation. Our results, summarized here, demonstrate that even small trees scattered in highly disturbed environments still offer habitat opportunities for a range of animal taxa

of scattered tree populations on the premise that isolated habitat resources located in hostile environments have limited value for biodiversity (Lindenmayer & Franklin, 2002; Manning, Lindenmayer, & Nix, 2004; Mendenhall et al., 2016). We recognize that our study did not record demographic data (e.g., incidents of breeding) and is unable to specifically evaluate how scattered trees contribute to viable wildlife populations. However, studies have found that scattered trees are used for breeding purposes by numerous taxa,

including birds, bats and arthropods (e.g., Carpaneto et al., 2010; Manning, Lindenmayer, & Barry, 2004; Rhodes & Wardell-Johnson, 2006; Stagoll et al., 2012).

Nature reserves play a crucial role in biodiversity conservation, and our results do not undermine this as some species recorded in our study may depend on large intact reserves for survival. However, reserves form only a small part of the wider landscape and alone are unlikely to be sufficient at conserving biological diversity (Franklin & Lindenmayer, 2009; Rayner et al., 2014). Scattered trees can help facilitate adaptive behaviours (e.g., dispersal and migration) that may contribute to species persistence across broader landscapes (Fischer & Lindenmayer, 2002b; Manning et al., 2009). We strongly encourage wildlife-orientated management directives that recognize the important biodiversity value of scattered trees. Conservation measures should prioritise scattered tree retention and perpetuation efforts in disturbed environments, which should complement reserve establishment and/or expansion strategies that are also recognized as important for biodiversity conservation.

Retaining scattered trees in modified landscapes requires a concerted effort to resolve conflicts of interest and mitigate and avoid the loss of established trees wherever possible (Le Roux, Ikin, Lindenmayer, Manning et al., 2015; Lindenmayer et al., 2013). For example, strategically planned urban developments could retain more existing trees in urban greenspace rather than removing trees at construction (Ikin et al., 2015; Le Roux, Ikin, Lindenmayer, Manning et al., 2014; Rayner et al., 2015). Retaining scattered trees can provide immediate habitat benefits to wildlife, while also being a more feasible conservation approach compared to ameliorating development impacts through costly biodiversity offset strategies like planting and maintaining large quantities of replacement seedlings (tubestock), purchasing "set-aside" reserve land or recreating mature tree structures such as artificial hollows (Gibbons & Lindenmayer, 2007; Le Roux et al., 2015; Lindenmayer et al., 2017; Maron et al., 2012; Vesk, Nolan, Thomson, Dorrough, & Mac Nally, 2008). Scattered trees can also serve as useful indicator structures of ecosystem function (Hunter et al., 2017; Lindenmayer, Margules, & Botkin, 2000; Tews et al., 2004). Conserving trees in disturbed landscapes can maintain high levels of biodiversity, which may also facilitate vital ecological services (e.g., pollination and seed dispersal; Herrera & García, 2009) that can ultimately provide numerous socio-economic benefits (e.g., arthropod pest control by birds and bats in agricultural land; Maas, Clough, & Tscharntke, 2013).

Our results highlight the importance of large old trees for birds. Habitat resources associated with large trees, such as hollows, accrue only over centuries and once removed are irreplaceable in the short-term (Manning et al., 2012). However, the biodiversity value of smaller sized trees should not be discounted in tree management policies. Revegetation efforts and affording protection to a range of tree sizes in modified landscapes are crucial for the long-term perpetuation of large old trees (Gibbons et al., 2008; Le Roux, Ikin, Lindenmayer, Manning et al., 2014).

Effective biodiversity conservation requires integrating wildlife response data into targeted management and habitat protection

policies, which should be implemented at multiple spatial scales. To better align conservation priorities for different taxa in modified landscapes, we recommend prioritizing the protection, retention and perpetuation of scattered trees of different sizes wherever possible, thereby providing crucial habitat opportunities for a multitude of taxa.

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BIOSKETCH

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