



Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets

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ABSTRACT

Land development contributes to the clearance of large trees that are sometimes offset with many smaller trees as compensatory wildlife habitat. But are many smaller trees a valid biodiversity offset for the loss of a single large tree? To answer this question, we tested predictions underpinned by island biogeography theory. Targeting birds, we investigated size and landscape context effects at 72 trees of three sizes (small, medium, and large) located in four landscape contexts (reserves, pasture, urban parklands, and urban built-up areas). Significant positive relationships occurred between tree basal area and bird abundance and species richness in all landscape contexts. SLOSS (single large or several small) analysis revealed that in modified landscapes, several small and medium trees supported an equivalent number of individuals and species as a single large tree, but the same pattern was weaker in reserves. Extrapolated rarefaction curves revealed that in reserves and urban built-up areas, many small or medium trees accumulated the same number or more species than large trees. However, in pasture and urban parklands, many small or medium trees accumulated fewer species than large trees. Overall, 29% of bird species were recorded only at large trees, highlighting that many smaller trees will not be suitable habitat compensation for all species. Complementary approaches to biodiversity offsets are needed, balancing large tree preservation and revegetation. Response patterns for birds at trees conformed to some biogeographic predictions (species–area relationship), but not others (habitat–isolation relationship), underscoring the need for novel conceptual frameworks for habitat structures in modified landscapes.

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1. Introduction

A major global conservation challenge is balancing biodiversity preservation with the intensification of human-led activities (e.g. agricultural and urban expansion; [Foley et al., 2005](#); [Grimm et al., 2008](#); [Tilman et al., 2011](#)). A vital step towards achieving this balance requires maintaining and appropriately managing critical habitat resources needed for species to persist ([Lindenmayer et al., 2006](#); [Le Roux et al., 2014a](#)). Large trees are one resource, which provide structural elements (e.g. hollows, woody debris) that many species depend on for survival ([Gibbons and Lindenmayer, 2002](#); [Nordén et al., 2004](#); [Ranius et al., 2009](#)). Large trees have been described as ‘keystone structures’ because they can be disproportionate providers of wildlife habitat relative to their size and availability ([Manning et al., 2006](#); [Fischer et al., 2010a](#); [Stagoll et al., 2012](#)).

Large trees are in decline due to anthropogenic pressures in ecosystems worldwide ([Lindenmayer et al., 2012](#)), including native forests ([Laurance et al., 2000](#)), agricultural landscapes ([Gibbons et al., 2008](#)),

production forests ([Stevenson et al., 2006](#)) and urban environments ([Le Roux et al., 2014b](#)). In modified landscapes, the persistence and management of large trees can be contentious as large trees may be perceived as ‘hazardous’ due to public safety risks (e.g. falling branches) or as ‘nuisance structures’ posing physical obstruction to urban development and agricultural practices ([Carpaneto et al., 2010](#); [Fischer et al., 2010b](#); [Stagoll et al., 2012](#)). As a result, the rate at which large trees are intentionally removed from modified landscapes typically exceeds the rate at which they are replaced ([Lindenmayer et al., 2013](#)). Large trees only form over extended time periods ([Ranius et al., 2009](#); [Cockle et al., 2011b](#)). Like other slow to mature, long-lived organisms (e.g. marine megafauna), the removal of large trees has long-term population implications ([Gibbons et al., 2008](#); [Manning et al., 2012](#)). Offsetting the loss of large trees by establishing many smaller trees is a management strategy that is now increasingly being employed ([Gibbons and Lindenmayer, 2007](#); [Maron et al., 2012](#)).

Biodiversity offsets is a policy instrument widely used in public and private sectors aimed at compensating for anthropogenic impacts by providing equivalent ecological gains ([ten Kate et al., 2004](#); [Business and Biodiversity Offsets Program \(BBOP\), 2012](#)). Direct offset strategies often seek to achieve no net loss of biodiversity by providing like for like habitat replacement at, or near, impacted sites ([Bekessy et al., 2010](#); [Gardner et al., 2013](#)). Typical land development scenarios involve

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clearing existing habitat, including large established trees, and subsequently planting many smaller immature trees as compensatory habitat (i.e. trading large old trees for small young trees; [Vesk et al., 2008](#); [Gibbons et al., 2010](#)). However, given the time lags involved in tree maturation and the set of unique structural attributes provided only by large trees (e.g. hollows), it has yet to be demonstrated that several smaller trees are a valid offset for the loss of a single large tree. Furthermore, tree clearance in degraded habitats (e.g. paddock trees) tends to be more commonly approved by legislation compared with intact habitats as it often assumed that isolated trees are less valuable for biodiversity than trees that form part of a patch ([Gibbons et al., 2009](#); [NSW Government, 2014](#)).

In this study, we asked: Are several smaller trees a valid biodiversity offset for the loss of a single large tree? We investigated whether fundamental ecological principles underpinned by the equilibrium theory of island biogeography ([MacArthur and Wilson, 1967](#)) and the SLOSS debate (single large or several small; [Simberloff and Abele, 1976](#)) provide a useful starting point to answer this question and inform biodiversity offset strategies in different landscape contexts.

Island biogeography theory ([MacArthur and Wilson, 1967](#)) predicts that: (1) larger habitat patches support more species and individuals than smaller patches (species-area relationship), which may partly be attributed to habitat heterogeneity or a greater diversity in habitat types as described by niche theory ([Hutchinson, 1959](#)); and (2) more isolated habitat patches support fewer species compared with more intact habitats (habitat-isolation relationship). These fundamental biogeographic principles have been successfully demonstrated for a wide range of organisms at many scales (e.g. [Lomolino, 1984](#); [Hanski et al., 1994](#); [Peay et al., 2007](#)). They also have been adapted and applied to on-the-ground conservation issues, most notably to reserve design ([Diamond, 1975](#)) but also to habitat restoration ([Holl and Crone, 2004](#)). In some cases, observed biological patterns do not always conform to predicted principles, which can make real-world applications challenging and controversial ([Laurance, 2008](#); [Fahrig, 2013](#)). This is exemplified by the SLOSS debate. Some argue that several small patches dispersed in space are more heterogeneous and have equal or more biodiversity value than a single large patch ([Simberloff and Abele, 1976](#); [Higgs and Usher, 1980](#); [Fischer and Lindenmayer, 2002c](#); [Oertli et al., 2002](#)). Alternatively, a single large patch may support unique species, maximise time to extinction, and maintain habitat structures and ecological processes that smaller patches cannot ([Diamond, 1975](#); [Patterson and Atmar, 1986](#); [da Silva and Tabarelli, 2000](#); [Beier et al., 2002](#)). As anthropogenic activities continue to fragment vast amounts of habitat worldwide ([Millennium Ecosystem Assessment, 2005](#)), conjecture remains about whether single large or several small habitat units are more preferable for biodiversity conservation ([Ovaskainen, 2002](#); [Tjørve, 2010](#); [Mendenhall et al., 2014](#); [Lindenmayer et al., 2015](#)).

Few studies have applied biogeographic principles and the SLOSS debate to tree-level biodiversity conservation ([Schei et al., 2013](#)). In modified landscapes, like agricultural and urban environments, scattered trees are often the units of habitat management (e.g. tree retention and removal policies; [Manning et al., 2006](#); [Stagoll et al., 2012](#)). Each individual tree essentially serves as an 'island refuge' surrounded by a landscape matrix or 'sea' with varying degrees of modification or 'hostility'. Larger trees differ from smaller trees in size and habitat heterogeneity due to the unique structures formed as trees age and senesce (e.g. hollows, woody debris and dead branches; [Gibbons et al., 2000](#)). In addition, interacting effects associated with the landscape context in which trees are located also likely drive response patterns at the tree-level (e.g. extent of human disturbance and the dispersal capacity of different species [Driscoll et al., 2013](#)).

We applied biogeographic principles and the premise of the SLOSS debate to data collected for birds at individual trees. Birds were targeted because they are easy to observe and studies have established relationships between tree occurrence and bird presence ([Fischer et al., 2010a](#);

[Stagoll et al., 2012](#)). Birds also represent a range of habitat, foraging and nesting guilds with many species dependent on tree resources (e.g. flowers, nectar and bark substrate [Fischer and Lindenmayer, 2002b](#)). Consistent with the theory of island biogeography, we hypothesised that: (1) significant positive relationships occur between tree size (basal area) and bird abundance and species richness with larger trees supporting more individuals and species than smaller trees; (2) trees located in a more intact landscape context (reserves) support greater bird abundance and species richness compared with more isolated trees located in modified landscape contexts (pasture, urban parklands and urban built-up areas); and (3) an offset strategy that retains a few large trees (>80 cm DBH) would be more beneficial for biodiversity than establishing many medium (50–80 cm DBH) or small trees (20–50 cm DBH).

2. Materials and methods

2.1. Study area

We conducted our study in and around the city of Canberra, Australian Capital Territory (ACT), southeastern Australia (35°17'35.64" S; 149°07'27.36" E). Canberra is situated in a highly fragmented landscape comprising: urban areas supporting 375,000 people; agricultural land for livestock grazing; and 34 nature reserves managed for conservation ([ACT Government, 2011](#)). Native *Eucalyptus* box-gum grassy woodlands once dominated the region but now persist mostly in reserves or as scattered paddock and urban trees ([Department of the Environment, 2015](#)).

2.2. Experimental design

We stratified our study region into four dominant landscape contexts representing varying degrees of modification: (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 in residential areas (e.g. roadside margins)). In each landscape context, we randomly selected six trees from three tree size categories: small (20–50 cm diameter at breast height (DBH)); medium (51–80 cm DBH); and large (≥ 80 cm DBH). Therefore, our design constituted four landscape contexts and three tree sizes each with six replicates resulting in a total of 72 sample trees. We restricted sampling to native *Eucalyptus* species. Sample trees were spaced >250 m apart to minimise spatial dependence and were located across nine reserves, four rural landholdings, 18 urban parklands and 18 urban built-up areas, which collectively spanned approximately 50 km². Importantly, 'small' trees were already established trees with heights of 12–17 m and canopy widths of 6–12 m. Trees <20 cm DBH (saplings and seedlings) were too small to be directly comparable as a 'tree' category. 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 ; $p > 0.05$; Kruskal–Wallis ANOVAs; see also Appendix A, Tables A1 and A2).

2.3. Bird surveys

We conducted four separate fixed point visual surveys at each of our 72 sample trees over two consecutive years (2012–13). Each survey was 20 min in duration (following [Fischer and Lindenmayer, 2002b](#)). This resulted in a total of 80 min of survey time per tree. Surveys involved sitting >5 m from each tree and recording the total number of individuals and species that came into direct physical contact with the tree. Surveys were undertaken in September and October of each year coinciding with the peak breeding period for birds in southeastern Australia (e.g. [Recher et al., 1991](#)). Surveys were undertaken by the same observer (DSL) between dawn and 11 a.m., avoiding unfavourable weather.

2.4. Data analyses

2.4.1. Basal area analysis

We calculated tree basal area from DBH measurements for all sample trees ($0.00007854 \times \text{DBH}^2$; Husch et al., 1993). Hence, tree sizes included: small ($0.05\text{--}0.19 \text{ m}^2$), medium ($0.20\text{--}0.49 \text{ m}^2$) and large trees ($0.50\text{--}2.30 \text{ m}^2$). We found significant positive relationships between tree basal area and tree height (Spearman's rho (correlation coefficient) = 0.67, t -value = 7.57, p -value < 0.001) and tree basal area and canopy width (rho = 0.84, t = 13.04, p < 0.001). We also found significant positive relationships between tree basal area and a range of tree-level habitat structures, including quantities of hollows, coarse woody debris, peeling bark substrate, mistletoe (epiphytes) and dead canopy branches (rho = 0.33–0.57, t = 2.02–4.99, p < 0.05). Therefore, tree basal area was a useful indicator of both physical tree size and tree habitat resources. We investigated the relationship between tree basal area and bird abundance and species richness using generalised linear regression models. We fitted basal area and landscape context in separate models for abundance and richness using a Poisson distribution with log-link function. Mantel tests confirmed no spatial autocorrelation occurred between sample trees for richness (r = 0.07; p = 0.06) and abundance (r = 0.04; p = 0.17). We also established linear species–area relationships between basal area and bird species in each landscape context.

2.4.2. SLOSS analysis

We used cumulative abundance–area and species–area curves to determine the relative contribution that small, medium and large trees made to bird abundance and species richness (Quinn and Harrison, 1988). All trees were first sorted by basal area. We then calculated the cumulative number of individuals and species when trees were sequentially added in ascending order of size (small trees added first). This was repeated with trees added in descending order of size (large trees added first). We repeated these analyses for five functional bird guilds based on differences in habitat, nesting and foraging traits (following Higgins et al., 2006).

2.4.3. Offset analysis

We used EstimateS (version 9; Colwell, 2013) to construct sample-based rarefaction curves for trees of different sizes in each landscape context. We constructed species accumulation curves based on the random selection of tree samples with 100 permutations without replacement (Colwell et al., 2004). Large tree samples in each landscape context had a greater cumulative basal area ($5.14\text{--}7.12 \text{ m}^2$) compared with medium ($1.72\text{--}2.40 \text{ m}^2$) and small tree samples ($0.56\text{--}0.83 \text{ m}^2$). To account for these differences, we extrapolated the number of medium and small tree samples until these each reached the same cumulative basal area of large trees sampled in each landscape context. To account for variation in basal area between individual trees, we randomly added samples with different basal areas selected from uniform distributions for medium and small tree size categories. We needed 7–15 additional medium trees and 34–54 additional small trees to reach the equivalent cumulative basal area of large trees in different landscape contexts. We also calculated offset ratios by dividing the mean number of individuals and species calculated for large trees by the mean number of individuals and species calculated for small and medium trees to estimate the minimum number of small or medium trees needed to support the same mean number of individuals and species as a single large tree. Values were rounded to the nearest whole number. For all analyses, data were pooled across survey years.

3. Results

We recorded 1188 individual birds identified to 55 bird species at our 72 sample trees (see Table A3 for recorded species and scientific names). At trees in reserves, pasture, urban parkland and urban built-

up areas, we recorded a total of 137, 379, 360 and 312 individuals and 27, 42, 28 and 25 species, respectively.

We found that 29% of bird species were recorded only at large trees (16 unique species). These species represented a wide range of functional guilds, including: woodland specialists (e.g. mistletoebird), hollow nesters (e.g. laughing kookaburra), arboreal nesters (e.g. olive-backed oriole), insectivores (e.g. satin flycatcher), granivores (e.g. little corella), nectivores (e.g. fuscous honeyeater) and threatened taxa (e.g. superb parrot). In comparison, we recorded 13% of species only at medium trees (seven unique species), while small trees contributed one unique species (1.8% of species). In reserves, pasture and urban parklands, we recorded 12 (45%), 19 (45%), and 13 (46%) unique species at large trees, respectively (Fig. A1). However, in urban built-up areas we recorded only one unique species at large trees (4%).

3.1. Basal area analysis

We found significant positive relationships between tree basal area and bird abundance (p < 0.001; Fig. 1a; Table A4) and tree basal area and bird species richness (p < 0.001; Fig. 1b). These relationships occurred irrespective of the landscape context in which trees were located (landscape context \times basal area, p > 0.05; see also Fig. A2 for log–log relationships between basal area and bird species in each landscape context). Significantly more individuals (p = 0.01) were recorded at trees located in modified landscape contexts (pasture, urban parklands and urban built-up areas) compared with trees located in reserves. For

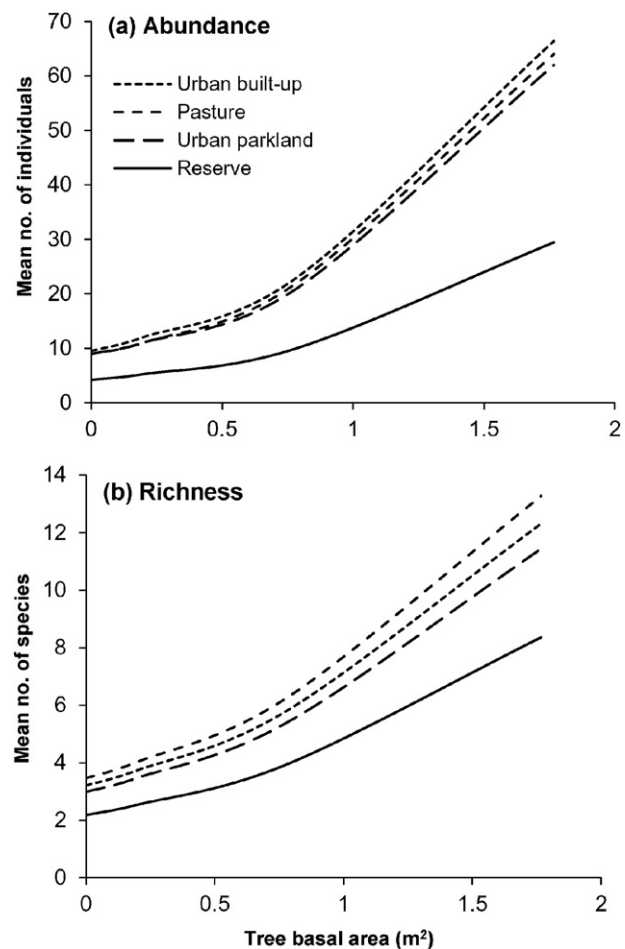


Fig. 1. Predicted relationships between tree basal area (m^2) and bird abundance (a) and species richness (b) in different landscape contexts (reserves, pasture, urban parklands and urban built-up areas). Basal areas indicated on the x-axes, 0, 0.5, 1, 1.5 and 2, correspond approximately to the following diameter at breast height (DBH, cm) values: 0, 80, 113, 138 and 160.

species richness, there was no significant difference in the number of species recorded between trees located in reserves and urban parklands ($p = 0.09$) and reserves and urban built-up areas ($p = 0.16$). However, significantly more species were recorded at trees located in pasture compared with reserves ($p = 0.04$). The deviance explained by basal area was 47% and 34% for abundance and richness models, respectively.

3.2. SLOSS analysis

In reserves (Fig. 2a) and urban built-up areas (Fig. 2d), abundance and species accumulation curves representing the addition of small trees first were situated above curves representing the addition of large trees first. In pasture (Fig. 2b) and urban parklands (Fig. 2c),

patterns differed as curves intersected and the amount of space between curves was reduced. In urban parklands (richness and abundance) and, to a lesser extent, in pasture (richness), adding large trees first tended to accumulate more individuals and species than adding small trees first. We also found that a single large tree supported the same number of individuals and species as several small and medium trees combined. This was especially evident in pasture, urban parklands and urban built-up areas (modified landscapes), but the same pattern was weaker in reserves. Large trees contributed the most individuals in all landscape contexts (reserves (58%), pasture (63%), urban parklands (70%) and urban built-up areas (51%)) compared with medium (25%, 31%, 16% and 35%) and small trees (17%, 6%, 14% and 14%). Large trees also contributed the most species in reserves (78%), pasture

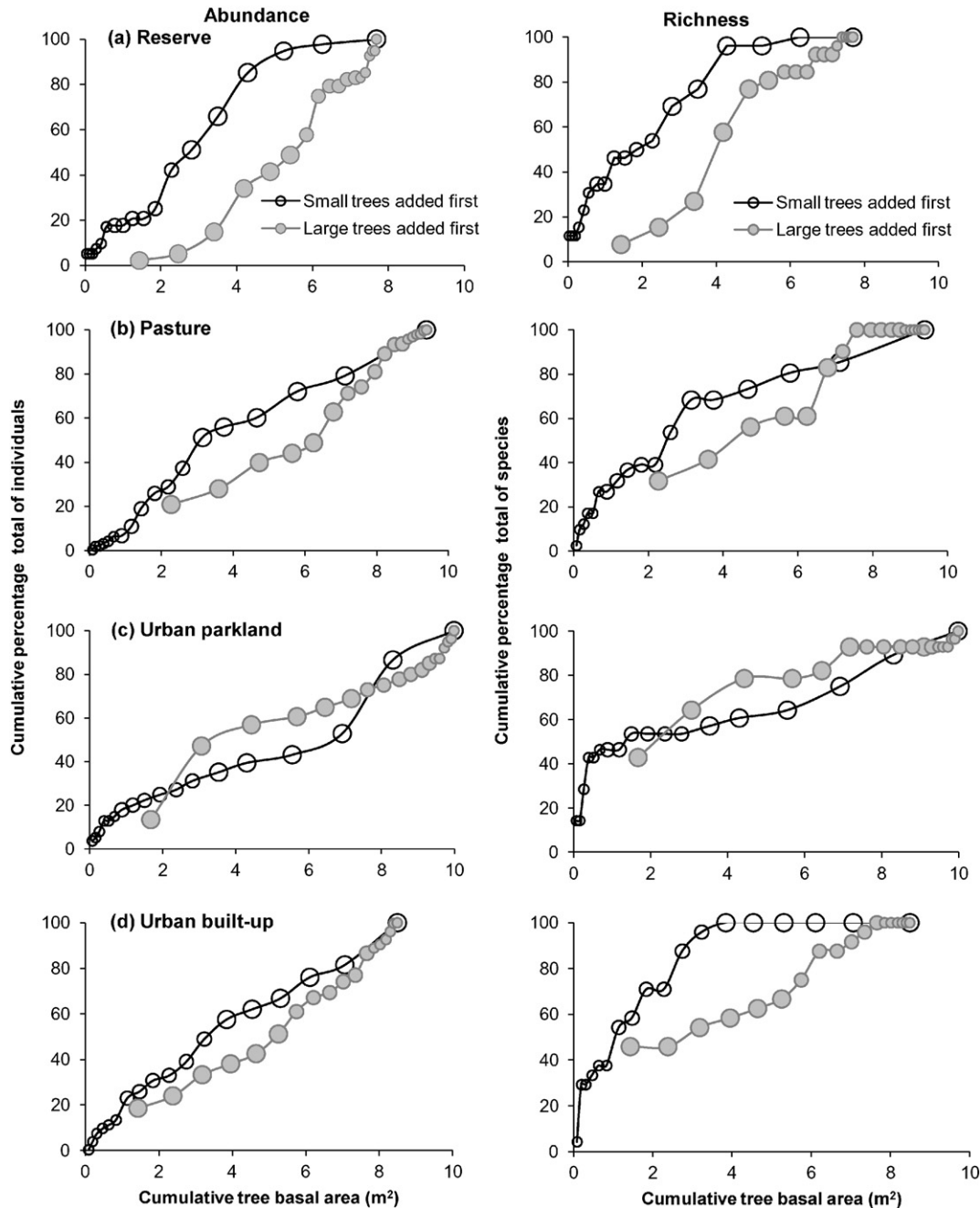
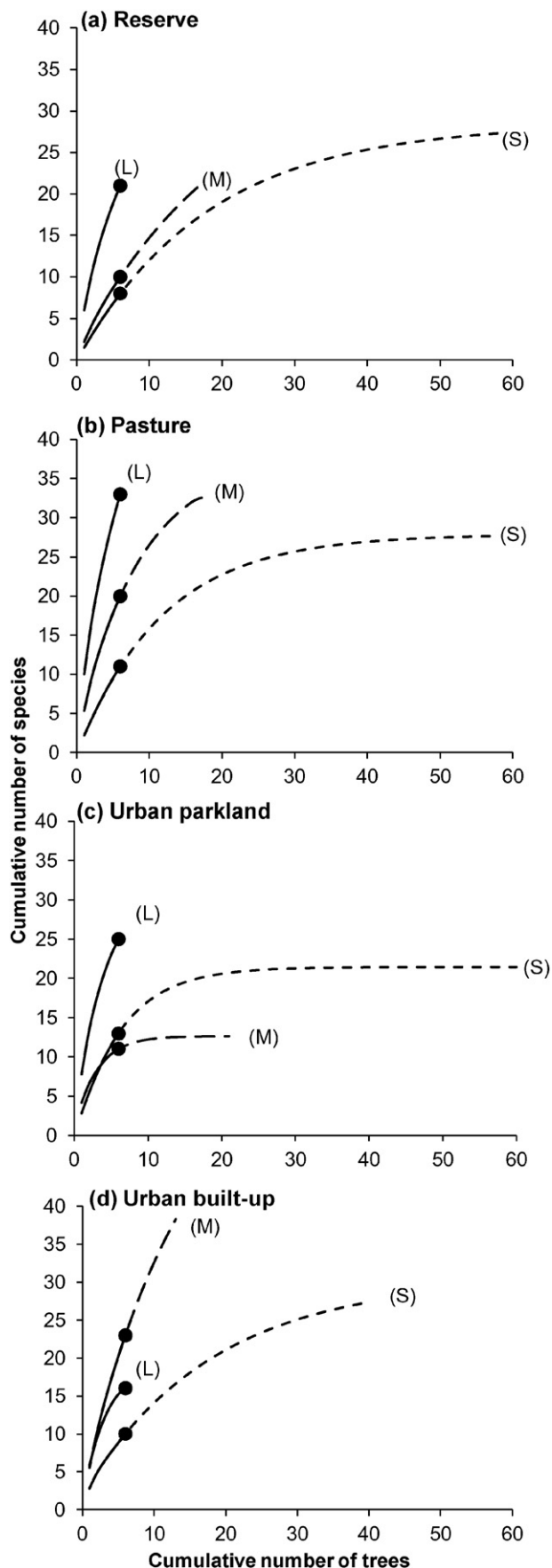


Fig. 2. Cumulative percentage total of individuals (abundance) and species (richness) plotted against the cumulative tree basal area (m^2) of sampled trees in each landscape context, including: reserves (a), pasture (b), urban parkland (c) and urban built-up areas (d). Plotted data represents the sequential addition of small trees first and the addition of large trees first. For each data series, marker sizes correspond to trees assigned to three pre-defined size categories including: small trees (20–50 cm DBH; $0.05\text{--}0.19\text{ m}^2$ basal area; smallest markers), medium trees (51–80 cm; $0.20\text{--}0.49\text{ m}^2$; medium sized markers) and large trees ($>80\text{ cm}$; $0.50\text{--}2.30\text{ m}^2$; largest markers).



(78%) and urban parklands (89%) compared with medium (37%, 48% and 39%) and small trees (30%, 26% and 46%). However, in urban built-up areas, medium trees contributed more species (92%) than large (64%) and small trees (40%). Guild analyses revealed that many small and medium trees contributed more strongly to the abundance and richness of woodland specialists, arboreal nesters and insectivores, but large trees contributed more strongly to the abundance and richness of granivores and hollow nesters (Fig. A3).

3.3. Offset analysis

Sample-based rarefaction curves revealed that small, medium and large trees did not accumulate species equally in different landscape contexts. In reserves, pasture and urban parklands, large trees accumulated more species most rapidly compared with medium and small trees (Fig. 3a–c). In these landscape contexts, rarefaction curves for small and medium trees reached or approached an asymptote but this was not the case for large trees. However, in urban built-up areas, medium trees accumulated more species most rapidly compared with large and small trees (Fig. 3d). In reserves and urban built-up areas, many small or medium trees accumulated the same number or more species than large trees when basal areas were equal. However, in pasture and urban parklands, many medium or small trees accumulated fewer species compared with large trees when basal areas were equal (Fig. A4 and Table A5). In reserves, pasture, urban parkland and urban built-up areas, the minimum number of offset trees that supported the same mean number of individuals and species as a single large tree was 4, 10, 5 and 4 small trees or 3, 2, 4 and 1 medium tree/s, respectively (Table 1). On average, more trees were needed to offset the habitat value of a large tree in pasture and urban parklands, compared with reserves and urban built-up areas.

4. Discussion

We tested three hypotheses to answer the question: Are many smaller trees a valid biodiversity offset for the loss of a single large tree? We found: (1) significant positive relationships between tree basal area and bird abundance and species richness, which was consistent with our first hypothesis and the predicted species–area relationship; (2) isolated trees located in modified landscape contexts (pasture, urban parklands and urban built-up areas) supported greater bird abundance and a similar or greater species richness than trees located in a semi-natural landscape context (reserves), which was inconsistent with our second hypothesis and the predicted habitat–isolation relationship; and (3) many smaller trees accumulated the same or more species as a few large trees in some landscape contexts (reserves and urban built-up areas), but not in others (pasture and urban parklands), which was only partially consistent with our third hypothesis.

4.1. Does tree size matter?

Our findings suggest that individual trees are partly analogous to habitat islands, as trees with larger areas supported significantly more individuals and species than trees with smaller areas (Fig. 1). Positive relationships between tree basal area and bird abundance

Fig. 3. Sample-based rarefaction curves for birds at trees of different sizes (small trees (20–50 cm DBH; 0.05–0.19 m² basal area; (S)), medium trees (51–80 cm; 0.20–0.49 m²; (M)) and large trees (>80 cm; 0.50–2.30 m²; (L))) located in different landscape contexts, including: reserves (a), pasture (b), urban parkland (c) and urban built-up areas (d). The interpolated cumulative number of species (solid lines) is plotted against the cumulative number of sample trees. Extrapolated species accumulation curves (broken lines) represent the number of additional small and medium sample trees added to achieve the equivalent cumulative basal area of large sample trees in each landscape context. Solid markers denote values derived from actual sample sizes.

Table 1

The estimated minimum number of small trees (20–50 cm DBH; 0.05–0.19 m² basal area) or medium trees (51–80 cm; 0.20–0.49 m²) needed to support an equivalent mean number of individual birds (abundance), bird species (richness) and basal area habitat (m²) as a single large tree (>80 cm; 0.50–2.30 m²) in different landscape contexts. Values were derived from mean one-to-one ratios and rounded to the nearest whole number.

Response	Landscape context			
	Reserve	Pasture	Urban parkland	Urban built-up
<i>Small trees:</i>				
Abundance	4	10	5	4
Richness	4	5	3	2
Basal area	10	10	11	6
<i>Medium trees:</i>				
Abundance	2	2	4	1
Richness	3	2	2	1
Basal area	3	4	3	2

and species richness were strong and consistent across all landscape contexts, suggesting that there are fundamental ecological processes underpinning these relationships at a tree-level. Physical attributes, like wide canopies and many lateral branches, likely make large trees visually prominent features in the landscape, which may act as attractive 'stepping stones' for birds (Fischer and Lindenmayer, 2002a; Manning et al., 2009). Large trees also may accommodate more individuals at any given time than smaller trees, which may be important to sustain bird populations (Stagoll et al., 2012; Barth et al., 2015). Furthermore, large trees support many habitat structures that smaller trees lack such as large quantities of peeling bark, flowers, nectar, epiphytes, litter, coarse woody debris, dead branches and hollows (Gibbons et al., 2000; Ranius et al., 2009; Lindenmayer et al., 2013). Heterogeneous structural elements at large trees provide crucial foraging and nesting resources for numerous bird species including rare and threatened taxa (Manning et al., 2006; Fischer et al., 2010a). Indeed, we found that large trees supported many more unique species (29% of all birds) than medium and small trees combined, which represented a diversity of functional guilds.

4.2. Does tree location matter?

Our findings highlighted that bird responses at individual trees are affected by the landscape context in which trees are located. Significantly fewer individual birds were recorded at trees located in reserves (a relatively intact environment), compared with scattered trees located in pasture, urban parklands and urban built-up areas (modified environments). Unlike islands, isolated trees actually attracted an abundance of birds. Therefore, we propose an alternative conceptual framework (Fig. 4a), which is more consistent with a diminishing returns model (Cunningham et al., 2014). That is, trees have a higher marginal value for birds inversely proportional to their availability. In modified landscapes, a reduced availability of trees due to anthropogenic pressures (e.g. tree clearance for development and cultivation; Le Roux et al., 2014a), likely means that isolated trees have become more valuable resources in higher demand by birds. Even smaller trees in a hostile landscape may be more attractive than smaller trees in a less hostile landscape where the value of each tree is effectively 'diluted' or spread among many trees that form part of an intact patch. Large trees in a hostile landscape, which provide additional structural complexity, may thus become disproportionate habitat 'hotspots' compared with smaller trees in the same environment and large trees in a less hostile environment.

For species richness, response patterns were more congruent with the intermediate disturbance hypothesis (Connell, 1978). More species were recorded at trees located in pasture compared with trees in reserves, urban parklands and urban built-up areas (see conceptual model displayed in Fig. 4b). Although agricultural

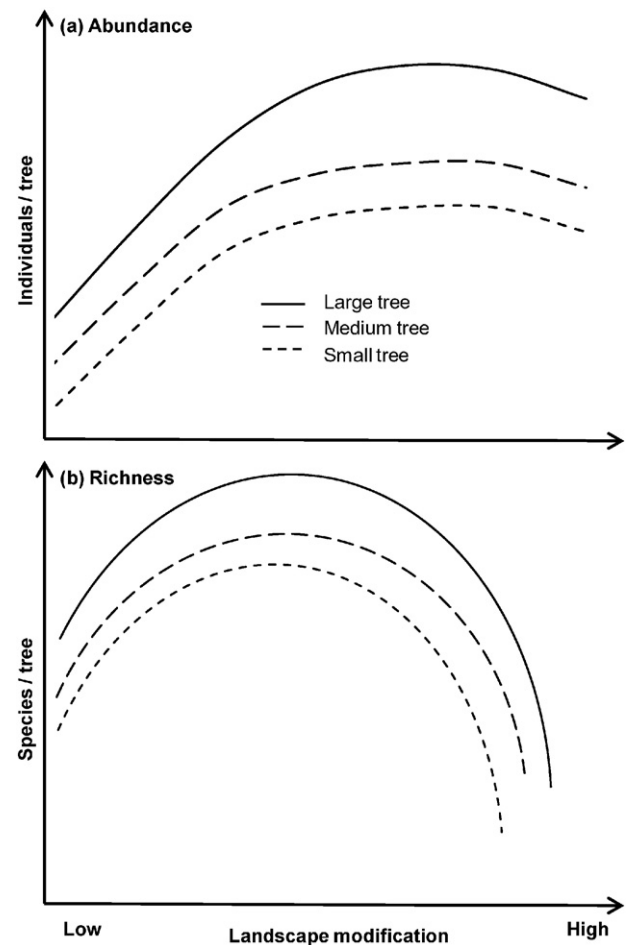


Fig. 4. Conceptual models showing bird responses at trees of different sizes located in landscape contexts with varying degrees of modification. Bird abundance (a) deviated from habitat-isolation predictions as more individuals were associated with trees located in modified landscapes (pasture, urban parklands and urban built-up areas). Bird richness (b) was consistent with the intermediate-disturbance hypothesis as more bird species were associated with trees in moderately disturbed landscapes (pasture and urban parklands). For richness and abundance, large trees tended to support more individuals and species than medium and small trees, consistent with species–area predictions. This explanatory framework provides a useful guide to tree management in modified landscapes and can inform biodiversity offset strategies where trees are used as 'tradable' habitat units. Biodiversity losses and gains are contingent on both tree size and landscape context factors and offset tactics should compensate for variation at these spatial scales to be effective at achieving no net loss.

landscapes are highly modified, they can cater to a diversity of taxa as they tend to maintain many resources also found in semi-natural reserves (e.g. fallen woody debris) and have fewer direct anthropogenic disturbances compared to urban habitats (e.g. traffic noise; Kato et al., 2009; Ikin et al., 2014b). Scattered paddock trees supported a mix of common (e.g. crimson rosella) and rarer species (e.g. scarlet robin; see also Fischer et al., 2010a). Trees in urban parklands also supported a mix of common (e.g. magpie lark) and rarer species (e.g. superb parrot; see also Stagoll et al., 2012). However, trees in urban built-up areas supported fewer, mostly urban-adapted species (e.g. red wattlebird). Trees in reserves supported some unique species (e.g. jacky winter), but 'dilution' effects likely reduced the probability of encountering many species at individual trees, especially where trees are clustered close together as part of continuous woodland habitat. Preserving trees in different land-use types will likely cater to the widest range of species that have varying sensitivities and dispersal capabilities (Marzluff and Ewing, 2001; Ikin et al., 2014a; Rayner et al., 2014).

4.3. Several small or single large?

We found that many smaller trees contributed strongly to bird abundance and richness, especially in reserves and urban built-up areas. Therefore, the collective habitat value of smaller trees should not be discounted. Many small and medium trees can capture greater geographical and microhabitat variation than a single large tree in one location (Schei et al., 2013). Accumulation curves for functional guilds also revealed that many small and medium trees contributed strongly to the abundance and richness of woodland specialists, arboreal nesters and insectivores. Birds in these guilds depend on foraging and nesting resources that are likely more widely available across a range of tree sizes (e.g. invertebrate prey and canopy branches for nest construction). Our results are consistent with other studies that have highlighted the biodiversity value of small isolated ponds (Oertli et al., 2002), woodland fragments (Fischer and Lindenmayer, 2002c) and grassland patches (Rösch et al., 2015) in modified landscapes.

We found considerable evidence of the conservation value of large trees, which contributed strongly to bird abundance and richness, especially in pasture and urban parklands. Large trees supported the most individual birds (51–70%) and a large percentage of bird species (64–89%) in all landscape contexts. Large trees also contributed strongly to the abundance and richness of granivores and hollow nesters (e.g. cockatoos and parrots), which may be especially limited by the availability of large hollows only associated with large trees (Cockle et al., 2011a; Manning et al., 2012). Furthermore, accumulation curves revealed that a single large tree located in modified landscapes (pasture, urban parklands and urban built-up areas) supported an equivalent number of individuals and species as many small and medium trees combined, but in a more intact landscape (reserves), these trends were weaker. This result re-iterates the high conservation value of large trees retained in modified landscapes, which is a finding that is in contrast to conservation priorities typically recommended at a patch-scale. For example, habitat suitability models for woodland birds suggest that increasing patch size for high quality habitat patches yields a greater return in species richness than increasing patch size in low quality habitat patches (Huth and Possingham, 2011). At a tree-level, we advocate that prioritising large tree retention in human-impacted environments can yield considerable biodiversity benefits.

4.4. Can many smaller trees offset a single large tree?

Given that the number of individuals and species supported by large trees differed with landscape context, it follows that the number of small or medium trees needed to offset the loss of a single large tree should also differ according to landscape context. In reserves, pasture, urban parklands and urban built-up areas, the minimum number of small and medium trees that supported the same mean number of individuals and species as a single large tree was 4, 10, 5 and 4 or 3, 2, 4 and 1 tree/s, respectively. Derived offset ratios that account for spatial context can serve as useful practical metrics that guide decision-making by practitioners who use trees as tradable units. However, simplistic offset metrics fail to explicitly account for unique species and may thus mask the exceptional value of large trees (Bekessy et al., 2010; Pilgrim et al., 2013). A further consideration is that the value of trees located in modified landscapes should not be overlooked.

In urban built up areas, we found that many medium or small trees accumulated the same number or more bird species than large trees when basal areas were equal. Therefore, many smaller trees can provide adequate habitat compensation equivalent to that of large trees for most bird species in this landscape context. Managing large trees safely in built-up residential areas can conflict with human interests such as public safety (Nagendra and Gopal, 2010; Hale et al., 2015). In turn, large trees may be frequently targeted for removal or may be highly managed with 'tidy-up' practices, thereby reducing structural complexity (e.g.

pruning dead branches; Terho, 2009; Le Roux et al., 2014b). This may explain why large trees in urban built-up areas accumulated fewer bird species compared to large trees located in other landscape contexts. Maximising tree 'subdivision' in residential areas by establishing many small and medium trees (e.g. along roadside margins) may thus be an effective and parsimonious offset strategy that balances the needs of people and wildlife. However, avoiding large tree removal in urban built-up areas can offer crucial habitat benefits for some species (e.g. hollow nesters) and support high bird abundance (Blewett and Marzluff, 2005; Barth et al., 2015). Where it is possible, strategic landscaping and spatial zoning tactics could be used to safely retain a few large 'wildlife' trees within urban built-up areas (Sandström et al., 2006; Le Roux et al., 2014a).

In urban parklands and pasture, we found that many medium or small trees were unable to accumulate an equivalent number of bird species as large trees. Therefore, offsetting the loss of a single large tree with many smaller trees is unlikely to be a sufficient habitat compensation strategy in these environments as the biodiversity gains are not commensurate to the losses incurred. That is, many bird species will not be adequately supported only by smaller trees. In urban parklands and agricultural land, space for trees may be particularly limited either by area (e.g. small pocket parklands) or because these environments are intensively managed for human purposes such as crop cultivation, livestock grazing or public recreation. Therefore, retaining a few large trees may be an effective management strategy in these environments, which can benefit many bird species but also maximise available space for human activities (Fischer et al., 2010b; Stagoll et al., 2012). However, large trees are often targeted for removal in urban parklands and agricultural settings and lack formal protection that recognises their disproportionate biodiversity value (Gibbons et al., 2009; Carpaneto et al., 2010). We advocate that strategic land planning and management policies are needed to avoid and minimise large tree removal wherever possible, especially where large trees are threatened by agricultural and urban expansion or infill practices (Lindenmayer et al., 2013). Managing a range of tree sizes in these environments is also important to ensure that tree populations are sustained over the long term (Gibbons et al., 2008; Le Roux et al., 2014b). Therefore, revegetation 'offsets' can be beneficial and would invariably outweigh the counterfactual (no offset), but our results indicate that these gains are likely to be inferior relative to large parkland and paddock tree retention.

It is important to recognise the risks associated with large tree removal. In particular: (1) large tree removal is likely to result in the loss of other crucial habitat structures (e.g. woody debris) and ecological processes (e.g. carbon sequestration) that cannot easily be replicated or restored (Gibbons and Lindenmayer, 2007; Maron et al., 2012); and (2) time lags between large tree removal and the maturation of smaller replacement trees is extensive (i.e. centuries) with a high risk of residual negative impacts persisting for large tree dependent biota (e.g. hollow-nesters) in the interim (Bedward et al., 2009; Manning et al., 2012). Managing delays between loss and gain by increasing the ratio of gain for each unit of loss (e.g. planting even more smaller trees for each large tree removed), may still be unable to ameliorate these impacts (Cunningham et al., 2007; Vesik et al., 2008). Practitioners need to establish replacement trees well in advance of scheduled impacts so that gains are functionally equivalent to the large tree losses incurred (Hilderbrand et al., 2005; Gibbons and Lindenmayer, 2007). Importantly, trees classified as 'small' in our study were well established (20–50 cm DBH). Some offset schemes may be based entirely on planted seedlings (<10 cm DBH) as the only habitat compensation, which may not even be suitable tree equivalents.

4.5. Conclusion

Biogeographic principles offer a useful starting point to test predictions related to species conservation at a tree-level. However, over-

extension of these principles should be met with caution. Responses observed for birds at individual trees conformed to species–area predictions, but not habitat–isolation predictions. Our results underscore the important biodiversity value of scattered trees. We have proposed novel conceptual frameworks for scattered trees which encapsulate observed tree size and landscape context effects for birds. Practitioners that use trees as ‘tradable’ conservation units in biodiversity offset schemes should aim to establish offsets for birds within modified landscapes. Careful attention to time lags and landscape context effects are also needed and tree management strategies should be adapted accordingly and in advance of development impacts to minimise risk. Ultimately, complementary approaches to tree management and biodiversity offsets are needed that balance large tree preservation (single large) and revegetation (several small).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2015.08.011>.

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