Maintaining and perpetuating habitat structures for wildlife in modified landscapes

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Cover images (clockwise from left): Large native tree, *Eucalyptus melliodora*, retained along a roadside verge in Canberra, Australia © Darren Le Roux; Helena gum moth, *Opodiphthera helena*, perched on bark © Darren Le Roux; Little forest bat, *Vespadelus vulturnus*, roosting under peeling bark © Darren Le Roux; Pair of Galahs, *Eolophus roseicapilla*, nesting in a tree hollow © Canberra Ornithologists Group, Inc.

Declaration

This thesis is my own work except where otherwise acknowledged.

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Preface

This thesis is structured as a compilation of six connected papers that have been published or have been submitted for publication in scientific journals. Each paper is a stand-alone body of work. However, there is unavoidable repetition of content and methodology between papers.

The formatting and content of my thesis complies with The Australian National University's College of Medicine, Biology and Environment guidelines. An Extended Context Statement has been provided at the beginning of the thesis, which provides a framework for understanding the relationship between the different components of my research and succinctly identifies broad themes that may be especially relevant for practitioners and applicable to other studies further afield. The Extended Context Statement is not intended to be a comprehensive literature review.

I completed the majority of the work, including: study design, data collection, laboratory work, data analysis and write-up. For all papers, I received advice from my supervisors: Associate Professor Philip Gibbons, Dr. Karen Ikin, Professor (AO) David Lindenmayer, and Associate Professor Adrian Manning. For paper I, I received statistical support from Wade Blanchard. For Papers V and VI, I received statistical support from Gideon Bistricer. All co-authors peer-reviewed written content and agreed to the submission of each paper. The author contribution statements below have been agreed to in writing by all authors listed. Detailed acknowledgments are provided at the end of each paper.

Paper I. Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Blanchard, W., Manning, A.D. & Gibbons, P. (2014). Reduced availability of habitat structures in urban landscapes: implications for policy and practice. *Landscape and Urban Planning*, 125, 57-64.

> Conceptualisation and design: DSL, KI, DBL, ADM, PG. Data collection: DSL. Data analyses: DSL, WB. Write-up: DSL. Editing: DSL, KI, DBL, WB, ADM, PG.

Paper II. Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2014). The future of large old trees in urban landscapes. *PLoS One*, 9(6), e99403, 1-11.

> Conceptualisation and design: DSL, KI, DBL, ADM, PG. Data collection: DSL. Data analyses: DSL, PG. Write-up: DSL. Editing: DSL, KI, DBL, ADM, PG.

Paper III. Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2015). The value of scattered trees for biodiversity: contrasting effects of landscape context and tree size. Under review: *Diversity and Distributions*.

> Conceptualisation and design: DSL, KI, DBL, ADM, PG. Data collection: DSL. Data analyses: DSL, KI. Write-up: DSL. Editing: DSL, KI, DBL, ADM, PG.

Paper IV. Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2015). Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets. *Biological Conservation*, 191, 558-566.

> Conceptualisation and design: DSL, KI, DBL, ADM, PG. Data collection: DSL. Data analyses: DSL. Write-up: DSL. Editing: DSL, KI, DBL, ADM, PG.

Paper V. Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Bistricer, G., Manning, A.D. & Gibbons, P. (2015). Enriching small trees with artificial nest boxes cannot mimic the value of large trees for hollow-nesting birds. *Restoration Ecology*, 24(2), 252-258.

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Paper VI. Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Bistricer, G., Manning, A.D. & Gibbons, P. (2016). Effects of entrance size, tree size and landscape context on nest box occupancy: considerations for management and biodiversity offsets. *Forest Ecology and Management*, 366, 135-142.

> Conceptualisation and design: DSL, KI, DBL, ADM, PG. Data collection: DSL. Data analyses: DSL, GB. Write-up: DSL. Editing: DSL, KI, GB, DBL, ADM, PG.

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There is a legion of Fenner School staff, volunteers and organisations that have helped with various aspects of my research – too many to mention here. However, I would like to thank Rob Thorman and Jess Stewart at the Land Development Agency for their partnership and support. I thank Piers Bairstow and Mauro Davanzo for their logistical support with fieldwork and Wade Blanchard and Gideon Bistricer for their statistical expertise. I also thank Clare Henderson, Kelly Debono, Chris Porter and Anna-lena Tews for their outstanding support in the field, even in the blistering sun.

I would also like to thank my peers at the Fenner School and further afield who have provided support and advice, including: Ben Scheele, Nelida Villaseñor, Clare Foster, Will Batson, Laura Rayner, Philip Barton, Laurence Berry, Marcos Tricallotis, Keshab Goutam, Pia Lentini, Tanja Straka and Kate Grarock.

Finally, thank you so much to my amazing family for their love, especially my wife, Noa, and daughters, Jade, Rhea and Ruby. You are my shining light and I could not have done this without you.

Abstract

Landscape modification is a major global threat to terrestrial biodiversity. Managing human-modified landscapes in ecologically sustainable ways is crucial to avoid and mitigate biodiversity loss. However, practitioners (e.g. policymakers and developers) still urgently require research to inform targeted habitat protection policies, on-the-ground land management practices, and biodiversity offset strategies.

My research focused on identifying ways to strategically maintain and perpetuate habitat structures for wildlife in modified landscapes. I had three objectives: (1) measure and compare the current and future availability of habitat structures; (2) quantify the biodiversity value of scattered trees; and (3) test the effectiveness of artificial nest boxes as a biodiversity offset tool.

First, I conducted vegetation surveys at 300 plots in three dominant landscape contexts (reserves, pasture, urban greenspace). I found that in urban greenspace, the availability of multiple habitat structures (e.g. trees, logs, shrubs) depended upon by biota were significantly reduced compared with reserves, but comparable with agricultural land. Using a simulation model for tree populations, I also found that hollow-bearing trees were predicted to decline by an average of 87% in urban greenspace over the next 300 years under existing tree management policies. I identified that only a combination of tree management approaches can arrest this decline.

Second, I completed wildlife surveys at 72 individual trees of three sizes (small, medium, large) located in four landscape contexts (reserves, pasture, urban parklands, urban built-up areas). I recorded high invertebrate, bat and bird abundance and richness at scattered trees, representing a diversity of functional guilds. Furthermore, the biodiversity value of scattered trees in modified landscapes, including even small trees, was comparable or greater than that of trees located in reserves. I also found that several smaller trees could provide habitat compensation equivalent to that of a single large tree for some bird species and in certain landscape contexts (reserves and urban built-up areas). However, this was not a suitable offset strategy for a quarter of bird species and in other landscape contexts (pasture and urban parklands).

Finally, I conducted an experiment using 144 nest boxes with different entrance sizes (20, 35, 55, 75, 95 and 115 mm), secured to trees of three sizes (small, medium, large) located in four landscape contexts (reserves, pasture, urban parklands, urban built-up areas). I found that adding nest boxes to large trees resulted in an increase in tree visitation by hollow-nesting birds. However, the same response was not observed at small, medium or control trees. Nest boxes were also only occupied by common native and exotic species and are thus unlikely to be effective at ameliorating the residual impacts of hollow-bearing tree removal, especially for threatened taxa.

Based on my collective findings, I recommend: (1) adopting spatial zoning tactics that aim to resolve human-habitat conflicts and retain multiple habitat structures; (2) prioritising the conservation of scattered trees over the long-term by balancing both re-vegetation and mature tree preservation strategies; and (3) exercising caution in the wide-scale application of nest box offsets. These recommendations could assist practitioners in establishing more biodiversity-sensitive modified landscapes.

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Extended context statement

Introduction

"The continued growth of human populations and of per capita consumption has resulted in unsustainable exploitation of Earth's biological diversity...more radical changes are required that recognize biodiversity as a global public good..." (Rands *et al*., 2010. p. 1298)

The impact of human activities on the natural environment is immense, long lasting and intensifying at unprecedented rates (Vitousek *et al.*, 1997; Lindenmayer & Fischer, 2013). Humans have had such a profound effect on the biosphere that many environmental scientists consider Earth to have entered a new epoch – the Anthropocene (Zalasiewicz *et al.*, 2011; Corlett, 2015). A defining hallmark of this era is the accelerated rate of human-induced biodiversity losses, estimated to be 100 to 1,000 times that of pre-human levels (Barnosky *et al.*, 2011; Dirzo *et al.*, 2014; Ceballos *et al.*, 2015). The single biggest environmental stressor driving terrestrial species losses is habitat destruction and fragmentation associated with land-use change (Sala *et al.*, 2000; Haddad *et al.*, 2015). In particular, urbanisation and agricultural intensification are the key underlying threatening processes that have collectively resulted in the conversion of tens of millions of hectares of habitat worldwide (Foley *et al.*, 2005; Grimm *et al.*, 2008). By 2050, it is estimated that 6.4 billion people will reside in cities (66% of the world population; United Nations, 2014), while global food demand could result in a further one billion hectares of habitat being converted for agricultural purposes (Tilman *et al.*, 2011). Never before has the future of biological diversity depended so much on how modified landscapes are managed.

The long-held assumption that modified landscapes are incompatible with biodiversity conservation has been a major barrier for developing progressive and innovative land management approaches in these environments (Lindenmayer & Franklin, 2002; Marzluff, 2002). This notion is also starkly reflected in the ecological literature with many research studies focusing on protected areas with low levels of human disturbance rather than on landscapes impacted by human activities (Miller & Hobbs, 2002; Fazey *et al.*, 2005). It is now widely acknowledged that nature reserves alone will be insufficient for conserving a majority of species, natural resources, and ecological processes (Daily *et al.*, 2003; Rodrigues *et al.*, 2004; Chazdon *et al.*, 2009; Cox & Underwood, 2011). As a result, conservation investments and priorities must transcend reserve boundaries and extend into landscapes that are altered and managed primarily for human purposes (McDonald *et al.*, 2008; Franklin & Lindenmayer, 2009). There are compelling arguments in favour of this redirection. Most of the world's biodiversity hotspots geographically overlap with major urban centres and agricultural areas (Myers *et al.*, 2000; Seto *et al.*, 2012). In turn, many threatened taxa persist in modified landscapes, which can provide important and novel habitat opportunities for species (Aronson *et al.*, 2014). Furthermore, the loss of biodiversity in modified environments can have serious long-term repercussions that affect vital ecosystem services (e.g. water quality) and human health and well-being (Díaz *et al.*, 2006; Flynn *et al.*, 2009). Renewed emphasis on species conservation in modified landscapes necessitates a fundamental shift in thinking from 'the battle has already been lost' to 'the battle has just begun'.

There are many inextricable conservation challenges in modified landscapes, some of which are unique to urban and agricultural settings. Direct and indirect impacts that can adversely affect biodiversity include: biotic homogenisation, proliferation of invasive species, edge-effects, soil erosion, noise and light disturbance, pesticide use, and pollution (Tscharntke *et al.*, 2005; McKinney, 2008). However, the loss and fragmentation of existing habitat is arguably the primary threat to most species (IUCN, 2015). To prospectively or retrospectively manage modified landscapes in biodiversity-sensitive ways requires provision and protection of the habitat resources that species depend on for survival (Rands *et al.*, 2010). This is a central but extremely complex challenge that is exacerbated by a plethora of social, economic and political constraints (Reyers *et al.*, 2010). Practitioners such as policymakers, developers, planners and landowners must find ways to balance conflicts of interest and seize opportunities to innovatively marry socio-economic and biodiversity objectives (Ikin *et al.*, 2015). To achieve this urgently requires research to guide and inform targeted habitat protection policies, on-the-ground land management practices, and biodiversity offset and restoration efforts.

The overarching objective of my research was to identify ways to strategically maintain and perpetuate habitat structures for wildlife in modified landscapes. I had three parts to my research spanning multiple spatial scales (Fig. 1): (1) I measured and compared the availability of habitat structures across dominant landscape contexts; (2) I quantified wildlife associations at individual trees; and (3) I tested the effectiveness of habitat supplementation using artificial nest boxes. My thesis provides an important contribution to the field of biodiversity conservation.

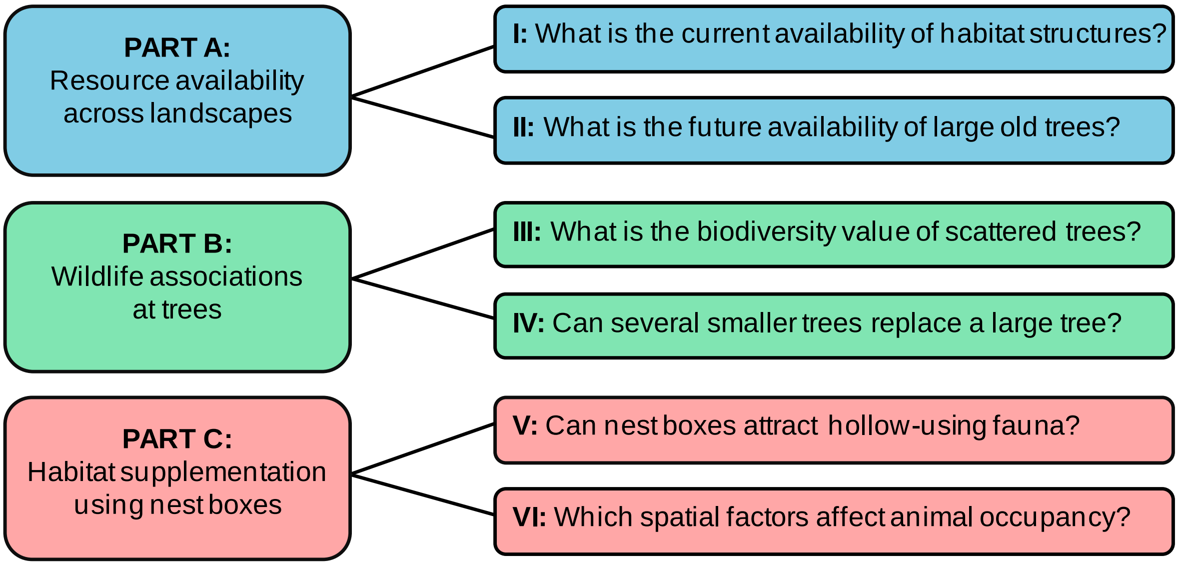

Figure 1. Thesis structure showing the sequence of research papers with key study questions.

Study area

I conducted my research 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 the ecologically diverse Southern Tablelands region west of the Great Dividing Range and is Australia’s eighth largest city encompassing an area of approximately 800 km^2 (ACT Government, 2011). The Canberra region is highly fragmented and comprised primarily of: urban areas supporting a population of approximately 380,000 people; agricultural land for livestock grazing; and 34 semi-natural nature reserves designated for conservation (Banks & Brack, 2003).

Summary of outcomes

Paper I: Reduced availability of habitat structures in urban landscapes: implications for policy and practice

In Paper I, I asked: what is the current availability of key habitat structures across dominant landscape contexts? Obtaining this baseline information is a necessary first step towards improving and developing targeted land management strategies (Lindenmayer *et al.*, 2008; Menz *et al.*, 2013). I conducted vegetation surveys at a landscape-scale to measure and compare differences in resource availability across nature reserves, pasture, and urban greenspace. I found that, in urban greenspace, the availability (density and / or probability of occurrence) of trees, seedlings, dead trees, hollow-bearing trees, hollows, logs and native ground and mid-storey vegetation were significantly reduced compared with reserves, but comparable with agricultural land. This finding underscores the urgent need for improved habitat protection policies in urban landscapes. In particular, I advocate that spatial zoning tactics could balance both socio-economic priorities and biodiversity conservation by minimising human-habitat conflicts in urban greenspace habitats (e.g. parklands and roadside verges). This may be an especially useful strategy for managing mature trees, which are often perceived as hazardous and targeted for removal in urban environments.

Paper II: The future of large old trees in urban landscapes

In Paper II, I asked: what is the future availability of large old trees in urban landscapes? Few studies have tracked changes in the availability of habitat resources over the long term (Gibbons *et al.*, 2008; Fischer *et al.*, 2010). Yet, this information is crucial to develop management directives that are focused on protecting and sustaining habitat structures in modified landscapes over extended time periods (Lindenmayer *et al.*, 2013). Using a dynamic simulation model for tree populations, I found that the number of hollow-bearing trees in urban greenspace is predicted to decline by an average of 87% over the next three centuries under existing tree management practices. To arrest and reverse this trajectory of decline requires an urban tree management strategy that collectively ensures: (1) tree standing life is maximised; (2) seedling recruitment is increased; and (3) the formation of habitat structures provided by large trees is accelerated (e.g. establishing artificial hollows such as nest boxes).

Paper III: The value of scattered trees for biodiversity: contrasting effects of landscape context and tree size

In Paper III, I asked: what is the biodiversity value of scattered trees? It is often assumed that isolated and small habitat resources, such as scattered trees, have less conservation value compared with resources located in more intact and larger patches. As a result, conservation efforts are often prioritised in nature reserves, while scattered trees in modified environments are frequently targeted for removal (Manning *et al.*, 2006; Gibbons *et al.*, 2009). I conducted a multi-taxonomic experiment to test the effects of tree location (landscape context) and tree size on wildlife abundance, richness and community composition. I found that landscape context and tree size affected different animal groups in complex and contrasting ways, which deviated from simplistic biogeographic predictions. Overall, I recorded high invertebrate, bat and bird abundance and richness at scattered trees, which represented a diversity of functional guilds. Scattered trees in pasture, urban parklands, and in urban built-up areas (e.g. roadside verges) retained disproportionate biodiversity value comparable to or greater than that of trees located in reserves. Conservation strategies should not discount the importance of isolated and small habitat structures located in human-modified landscapes.

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

In Paper IV, I asked: are many smaller trees a valid biodiversity offset for the loss of a single large tree? Land development often contributes to the clearance of large established trees that are subsequently offset with many smaller trees as compensatory habitat for wildlife (Gibbons & Lindenmayer, 2007; Vesk *et al.*, 2008). However, it has yet to be determined if many smaller trees support an equivalent abundance and species richness as a single large tree. Guided by the premise of the SLOSS debate (single large or several small; Diamond, 1975), I tested the effects of landscape context and tree size using birds as a target group. I found that larger trees supported significantly greater bird abundance and species richness than smaller trees. Many smaller trees were able to support an equivalent number of bird species as large trees in some landscape contexts (reserves and urban built-up areas), but not in others (pasture and urban parklands). Furthermore, almost a third of all bird species were recorded only at large trees. These findings suggest that complementary approaches to biodiversity offsets are needed, balancing both mature tree preservation and revegetation.

Paper V: Enriching small trees with artificial nest boxes cannot mimic the value of large trees for hollow-nesting birds

In Paper V, I asked: can the addition of artificial nest boxes at individual trees attract hollow-nesting fauna? A restoration strategy gaining popularity in modified landscapes involves adding nest boxes to smaller sized trees to replicate natural hollows that are typically only associated with large old trees. However, few studies have examined how wildlife might respond to hollow supplementation at broader scales (Berthier *et al.*, 2012; von Post & Smith, 2015). I conducted a before-after control-impact (BACI) nest box addition experiment and measured changes in hollow-nesting bird visitation at individual trees. I found that hollow-nesting bird abundance and species richness significantly increased at large trees after nest boxes were added. However, the same response was not observed at medium, small or control trees. These results suggest that artificially replicating hollows at smaller trees may not be sufficient to attract hollow-using fauna. Instead, large tree retention remains crucial and should be a management priority.

Paper VI: Effects of entrance size, tree size and landscape context on nest box occupancy: considerations for management and biodiversity offsets

In Paper VI, I asked: does entrance size, tree size and landscape context affect nest box occupancy outcomes? Nest boxes are often used to ameliorate the residual impacts associated with the loss of hollow-bearing trees. However, the effectiveness of nest boxes as compensatory nesting habitat for hollow-using species remains controversial and equivocal (Lindenmayer *et al.*, 2009; Goldingay *et al.*, 2015). Improving offset programs requires empirical research to identify spatial factors that influence nest box selection and use by wildlife. I found that nest box entrance size had a significant effect on occupancy, but tree size and landscape context did not affect occupancy. Furthermore, only common native and exotic mammal, bird, and invertebrate species occupied nest boxes. These findings suggest that practitioners who use nest boxes as applied conservation tools must pay particular attention to fine-scale nest box design attributes. My results also suggest that nest boxes are unlikely to be effective management and biodiversity offset tools, especially for threatened taxa. Therefore, avoiding the loss of hollow-bearing trees should be a high priority.

Synthesis

A recent report by the International Union for Conservation of Nature (IUCN) highlighted that the primary threat to 85% of Red Listed species is habitat loss (IUCN, 2015). This statistic calls to attention that global efforts to conserve biodiversity require a strong focus on how to appropriately manage habitat resources that are needed for species to persist. My research has demonstrated that this objective is especially pertinent and urgent in modified landscapes where human impacts on existing habitat are numerous, varied, and complex. From my collective research studies, I have identified three important themes or ‘take home’ messages that are highly relevant for practitioners.

1. Scale matters

The management of habitat resources in modified landscapes must be approached in an expansive way that is reflective of the different scales of biological organisation (Poiani *et al.*, 2000; Lindenmayer & Franklin, 2002). It is crucial for practitioners to formulate spatially explicit management strategies that have targeted operational methods to capitalise on limited resources such as funding (Goddard *et al.*, 2010; Gonthier *et al.*, 2014). For example, fine scale management initiatives (e.g. limiting the pruning of tree branches in suburbs; Paper I) may not adequately address broad scale problems (e.g. the decline of hollow-bearing tree populations; Paper II). Similarly, broad scale policy may not adequately address local problems. My findings have demonstrated that a multi-scaled management approach is essential to effectively maintain, offset, and restore habitat structures for wildlife in modified environments. At a landscape scale, I have highlighted that it is important to broadly identify resource limitations and formulate widely applicable management policies such as habitat protection legislation and land zoning tactics (Papers I and II). At a local scale, I have demonstrated that an understanding of how species interact with specific habitat elements, such as scattered trees of different sizes, can inform localised management efforts, such as tree retention and revegetation strategies (Papers III and IV). At a finer scale, I have shown that knowledge of how specific habitat attributes (e.g. nest box entrance size) affect species responses can also improve key conservation actions (e.g. designing artificial resources that better reflect the form of natural structures; Papers V and VI).

2. One size does not fit all

Wildlife interacts with the surrounding landscape and uses different habitat structures in complex ways that are often not congruent across taxa (Tews *et al.*, 2004; Hagen *et al.*, 2012). Therefore, it is important for practitioners to develop and apply habitat management strategies that focus on multi-taxonomic outcomes (Benton *et al.*, 2003; Beninde *et al.*, 2015). For example, I found that some species may effectively exploit resources in urban landscapes but other species may be adversely affected by anthropogenic disturbances in the same environment, highlighting the need to retain a mosaic of land-use types to benefit many species (Paper III). At a finer scale, I showed that hollow-using fauna preferentially occupy nest boxes with entrance sizes that are proportional to their body size, highlighting that both smaller and larger entrance sizes are needed to accommodate species with different nesting requirements (Paper VI). However, nest boxes may not benefit many hollow-using species, highlighting the importance of preserving and perpetuating hollow-bearing trees. My findings highlight that often complementary and cross-sectional approaches that balance a variety of management strategies are needed to account for the needs of a diverse range of biota. My findings have also emphasised that many conservation priorities underpinned by theoretical biogeographic principles (e.g. habitat-isolation relationship) may not be substantiated in modified landscapes (Papers III and IV). For example, even small isolated trees can be valuable for some taxa and can support greater wildlife abundance and species richness than trees located in semi-natural reserves. This finding suggests that novel wildlife-oriented management frameworks are needed that prioritise habitat preservation and restoration efforts within modified landscapes and rethink traditional uniform conservation targets.

3. Today's actions, tomorrow's outcomes

Accounting for time lags in the provision of habitat structures is paramount to successfully achieving ecologically sustainable outcomes in modified landscapes (Gibbons & Lindenmayer, 2007; Vesk *et al.*, 2008). It is important for practitioners to recognise that early intervention is crucial and that delays in the implementation of appropriate habitat management strategies invariably have long term conservation implications (Kuussaari *et al.*, 2009; Manning *et al.*, 2012). My results have demonstrated that to arrest predicted declines in habitat structures that form over extended time periods, such as hollow-bearing trees, collective management strategies need to be promptly mandated and implemented to mitigate and avoid adverse long term consequences for biodiversity (Paper II). My findings have also highlighted the risks associated with *status quo* land management, biodiversity offsets, and habitat restoration practices. For example, simply removing and replacing large trees with many smaller trees will not be a suitable habitat compensation strategy for almost a third of all bird species (Paper IV). Furthermore, habitat structures such as tree hollows cannot be easily replicated in the short term using artificial nest boxes, which are unlikely to fulfil a functionally equivalent role as natural hollows (Papers V and VI). I advocate that a stronger emphasis on large tree retention remains crucial and should be prioritised. However, to ensure that large trees and their associated habitat structures (e.g. hollows) are managed in perpetuity also requires preserving a range of tree sizes and investing in tree recruitment.

Concluding remarks

My research has provided important insights into the challenges and opportunities associated with biodiversity conservation in urban and agricultural landscapes. I have developed and explored a range of alternative management strategies that are needed to maintain and perpetuate habitat structures for wildlife in human-dominated environments. My results have underscored the importance of implementing innovative and transdisciplinary approaches to natural resource management across varying spatial and temporal scales. I have argued that complacent and expedient conservation decisions that focus primarily on short term gains must be substituted with strategic habitat management approaches that are accountable for long term impacts on biodiversity. Finding ways to balance human use and biodiversity value and integrate socio-economic priorities with habitat preservation objectives is crucial. This requires fostering dialogue and collaboration between multiple stakeholders including research scientists, government officials, developers, planners, land owners, and urban communities.

Future research is needed to provide more comprehensive assessments into the economic outcomes (e.g. cost-benefit analyses) and social perceptions (e.g. public awareness and acceptance) associated with managing habitat resources more naturalistically in shared spaces. Furthermore, long term experimental studies are required to measure changes in wildlife responses following the retention or artificial supplementation of key habitat elements (e.g. logs). Studies that establish linkages between habitat structures, wildlife response patterns, human well-being, and ecosystem services (e.g. soil nutrients, carbon storage, crop pollination) are especially pivotal in aligning biodiversity conservation priorities with social, economic, and political agendas. Ultimately, evidence-led biodiversity conservation must continue to be extended and accentuated in our farmlands, parklands, roadside margins, and backyards.

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Paper I. Reduced availability of habitat structures in urban landscapes: implications for policy and practice

Practitioners often lack broad-scale empirical data on the extent to which habitat structures have been modified or reduced. In Paper I, I measured and compared the availability of multiple habitat structures across dominant landscape contexts. This is a crucial starting point to identify limitations in natural resource availability and to formulate strategic land management policies and practices.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Blanchard, W., Manning, A.D. & Gibbons, P. (2014). Reduced availability of habitat structures in urban landscapes: implications for policy and practice. *Landscape and Urban Planning*, 125, 57-64

Abstract

Over half the world's population resides in cities, with increasing trends towards urbanisation expected to continue globally over the next 50 years. Urban landscapes will be more ecologically sustainable where key habitat structures (e.g. trees, shrubs and woody debris) that support multiple taxa are maintained. Yet, there is little empirical data on the extent to which habitat structures have been modified in urban landscapes. Obtaining these data is a necessary first step towards reducing the ecological impacts of urbanisation. This is because urban practitioners can use this information to formulate more targeted management policies and conservation strategies that seek to better maintain and perpetuate habitat structures in urban landscapes. We compared the availability of multiple habitat structures in urban greenspace, agricultural land, and semi-natural reserves in Canberra, southeastern Australia. In urban greenspace, the density and/or probability of occurrence of trees, seedlings, dead trees, hollow-bearing trees, hollows, logs and native ground and mid-storey vegetation were significantly lower compared with reserves, but comparable with agricultural land. Our results highlight an urgent need for improved habitat protection policies, management strategies, and on-the-ground conservation actions that aim to retain and restore key habitat structures in urban landscapes. To achieve this requires innovative strategies that balance socio-economic priorities and biodiversity conservation. We propose three strategies that can be practically implemented in cities worldwide including: (1) establishing dedicated conservation areas; (2) spatially zoning habitat structures hazardous to humans within existing urban greenspaces, and (3) educating key stakeholders about the importance of habitat structures within urban environments.

Keywords: biodiversity; human-habitat conflict; southeastern Australia; urbanisation; urban conservation planning; urban greenspace

Introduction

Habitat loss through land-use change is the biggest driver of terrestrial biodiversity decline globally (Pimm and Raven, 2000; Foley et al., 2005). Land conversion is driven by agricultural and urban expansion, the latter now occurring at unprecedented rates (UN, 2011). Urbanization is a complex process of land conversion, densification and hard-scaping that has been identified as one of the most rapid and destructive forms of landscape alteration (e.g. Grimm et al., 2008). Over half the world's population now resides in cities, with the global shift to urban living expected to continue over the next half century (UNDP, 2011). A major concern is that many urban areas around the world are disproportionately located in biodiversity-rich regions (e.g. McDonald et al., 2008). Therefore, it is increasingly important that biodiversity conservation be integrated into urban planning and development strategies to establish more ecologically sustainable urban landscapes (e.g. Rookwood, 1995). An important step towards achieving ecologically sustainable urban landscapes involves strategically managing and maintaining crucial habitat structures in urban contexts.

Trees, shrubs and associated structures, including hollows and woody debris, represent critical habitat for many species (e.g. Gibbons and Lindenmayer, 2002; Lindenmayer et al., 2012). These structures provide important sources of food, shelter, nesting sites, and structural complexity that a diverse range of taxa depend on for survival worldwide, including microbes (Hendrickson, 1991), plants (e.g. Kruys and Jonsson, 1999), invertebrates (e.g. Kaila et al., 1997), and vertebrates (e.g. Webb and Shine, 1997). The loss of habitat structures from modified landscapes is of increasing concern because of the negative consequences for both biodiversity and underpinning ecological processes such as nutrient cycling and carbon sequestration (e.g. Fischer et al., 2010a; Stagoll et al., 2012b and references therein). Ultimately, this also may have implications for human well-being (e.g. Díaz et al., 2006).

Maintaining habitat structures for biodiversity in cities can conflict with underlying political and socio-economic drivers of urban expansion (e.g. population growth), including policies that promote public safety and 'sustainable' urban growth (e.g. Stagoll et al., 2012b). For example, wood decay and canopy senescence in mature trees are key processes that form hollows and woody debris important for wildlife (Gibbons and Lindenmayer, 2002). However, these processes also may increase the risk of falling limbs in existing urban greenspace, which may harm people and property and result in managed tree removal (e.g. habitat tree removal in Rome, Italy; Carpaneto et al., 2010). Similarly, compact residential living is encouraged to reduce urban sprawl (Burgess, 2000), but this can lead to the in-fill of greenspace that might otherwise serve as wildlife corridors and refuges within built-up environments (e.g. parkland values to birds in Pachuca, Mexico; Carbó-Ramírez and Zuria, 2011). Given that these challenges occur in cities throughout the world, knowledge of current resource gaps in urban environments is urgently needed to better focus conservation efforts and improve methods of managing important habitat structures that cater to human interests while maintaining biodiversity values.

In this study we asked: What is the availability of habitat structures in urban landscapes and how does this compare with agricultural land and semi-natural reserves? A better understanding of current resource limitations in urban landscapes is a crucial first step in formulating more targeted land management policies, urban design strategies, and on-the-ground conservation actions (e.g. McDonnell & Hahs, 2013). This baseline information from primary data is typically unavailable to urban practitioners worldwide because few studies have empirically quantified the availability of habitat structures in urban environments at a landscape scale. We hypothesised that land management practices have led to significant reductions in the availability of habitat structures in urban landscapes compared with semi-natural reserves that are managed for conservation purposes. We also predicted that urban resource limitations would be comparable with agricultural land where the impacts of human-induced land modification on habitat resources has already been well demonstrated (e.g. Gibbons et al., 2008b; Fischer et al., 2009). Our study has global policy relevance and practical conservation implications for the current management of habitat structures in urban landscapes and for biodiversity conservation.

Methods

Study area

We conducted our study in and around the city of Canberra, Australian Capital Territory (ACT), southeastern Australia. Canberra covers an area of 810 km^2 and supports a population of 375,000 people, which is projected to double by 2056 (ACT Government, 2011). The city is highly planned and described as the “Bush Capital” due to the extensive suburban tree cover and 34 nature reserves flanking the urban boundary. The Canberra region was once dominated by box-gum *Eucalyptus* woodlands. However, land clearance for farming and urban development has led to approximately 95% decline in intact box-gum woodland, resulting in the listing of this ecological community as critically endangered in State and Federal legislation (Department of Environment and Heritage, 2006).

Sampling design

We confined our sampling to a single vegetation type: the predicted pre-European (pre-1750) extent of box-gum woodland within our study landscape. Within this vegetation type, we stratified our sampling according to three dominant land-use types and five geographical zones (Figure 1). The three land-use types selected are broadly represented in other human-modified landscapes globally (e.g. Foley et al., 2005) and included: (1) reserves (semi-natural conservation areas); (2) pasture (grazed agricultural land); and (3) urban greenspace, defined as publicly accessible areas constituting parklands (60%), roadside margins (24%), remnant vegetation (9%), and sports grounds (7%). Urban greenspace accounted for 11% of the total urban environment in our study area. To ensure that we captured variability across the landscape and to avoid biasing sampling effort to areas with specific local or historical attributes (e.g. fire history, grazing intensity), we also divided Canberra into five geographical survey zones.

We randomly allocated an equal number (n = 20) of fixed area plots (50 x 20 m; 0.1 ha) to each of the 15 strata. We had an equal number of plots per geographic zone (n = 60) and land-use type (n = 100), resulting in a total of 300 plots or 30 ha of sampled land from 28 reserves, 20 agricultural holdings, and 100 urban greenspaces. Plots were > 250 m apart to minimise spatial dependence and allocated to habitats ≥ 0.2 ha in size.

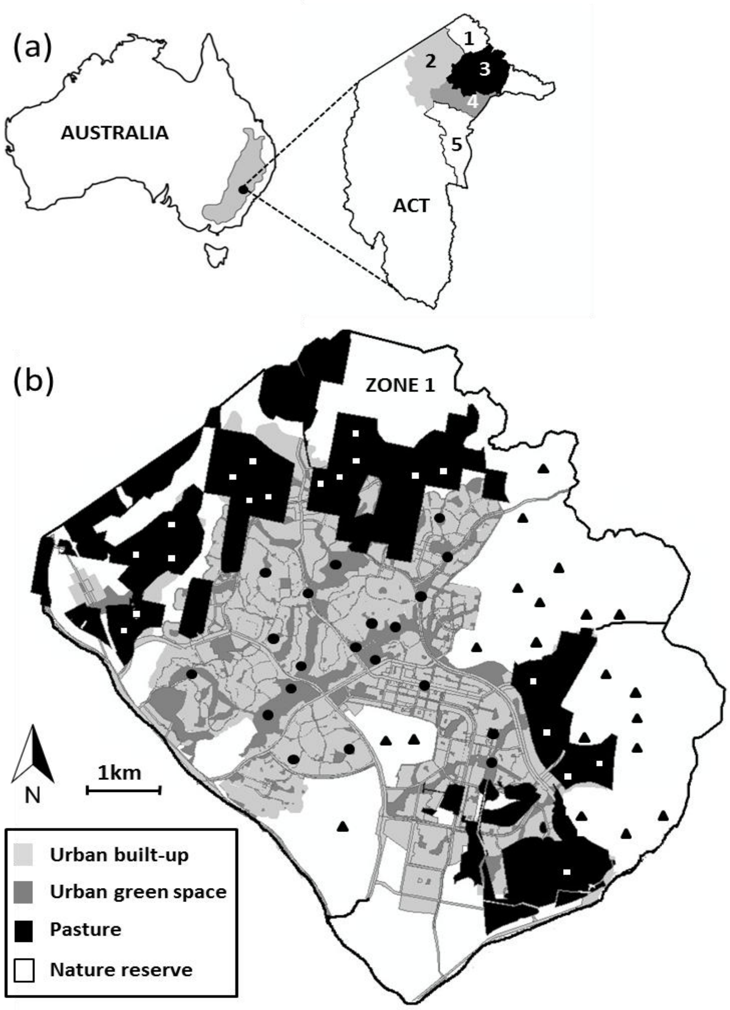

Figure 1. Map of Australia with pre-1750 extent of box-gum grassy woodland (shaded area) and the Australian Capital Territory (ACT), highlighted to show Canberra broken into five geographical survey zones (a). Detailed perspective of zone 1 shows the stratification of the landscape into current dominant land-use types with random allocations of 20 plots to reserves, pasture and the urban greenspace (b).

In each plot, the following habitat structures were measured: trees (native and exotic species with stems > 10 cm diameter at breast height over bark (DBH)), seedlings (trees with stems ≤ 10 cm DBH), dead trees, mature trees (trees with stems ≥ 50 cm DBH), hollow-bearing trees, hollows, logs, and ground and mid-storey cover (see Table S1 for the sampling methods associated with each habitat structure).

Statistical analyses

To assess the effect of land-use on the availability of each habitat structure, we used zero-inflated conditional regression models in GenStat (14th edition; VSN International Ltd). Count data had over-dispersed distributions with extra zeros resulting in possible extra-Poisson variation (Welsh et al., 1996). Zero-inflated conditional regression deals with over-dispersion by modelling response variables in two separate states: a binary state, where the presence of habitat structures is modelled (referred to here as probability of occurrence); and a count state, where the number of habitat structures occur with varying levels of abundance when encountered (i.e. conditional density, referred to here as density). Binomial models with a logit-link function were fitted for the binary state and truncated Poisson and negative binomial distributions with log-link functions fitted for the count state. By assessing residual deviances from Poisson models, we determined model distributions (i.e. Poisson or negative binomial) of best fit for each variable. Land-use and geographical zone were fitted as fixed effects. Geographical zone served as a proxy for other nested covariates (e.g. geology, tree planting history) that likely drive local difference in the availability of habitat structures. The effect of land-use was assessed via a likelihood ratio test statistic for the binary and count models (Table S2). For differences between urban greenspace (i.e. the model constant) and reserves and pasture, we derived Z-statistics and two-tailed probabilities from parameter estimates and standard errors for both the binary and count model states. For ground and mid-storey categorical data, we fitted logistic regression models with binomial distributions and logit-link functions for each category. Land-use and geographical zone were fitted as fixed effects.

Results

The availability of all habitat structures differed significantly ($P < 0.0001$) between land-use types (see Table S2 for summary statistics). However, the extent and nature of this difference was variable for individual structures (Fig. 2).

Living trees

We measured 5,602 stems belonging to 37 species (see Table S3 for a list of all recorded tree species in each land-use type). These constituted 3,935 (70%) seedlings (trees with stems ≤ 10 cm DBH) and 1,667 (30%) trees (stems > 10 cm DBH). Exotic species accounted for 30% of all recorded trees > 10 cm DBH in urban greenspace, but were not recorded in pasture and reserves. The density and probability of occurrence of trees in urban greenspace, for all species and native species only, was significantly lower ($P < 0.0001$) than in reserves (Figure 2a). The density of trees in urban greenspace was significantly higher ($P < 0.05$) than in pasture, but the probabilities of tree occurrence did not differ significantly between these land-use types ($P = 0.406$).

Tree regeneration

The density of seedlings in urban greenspace was significantly lower ($P < 0.0001$) than in reserves and pasture ($P < 0.001$; Figure 2b). Urban greenspace and pasture supported 18% of all seedlings recorded in our study landscape. Urban regeneration was dominated by native seedlings (72%) with 15% and 20% of plots having re-planted and naturally regenerating native trees, respectively. Twelve per cent of plots with seedlings in urban greenspace had evidence of protection measures for young trees (e.g. supporting posts or stem sheaths). This is compared to 3% of plots in pasture.

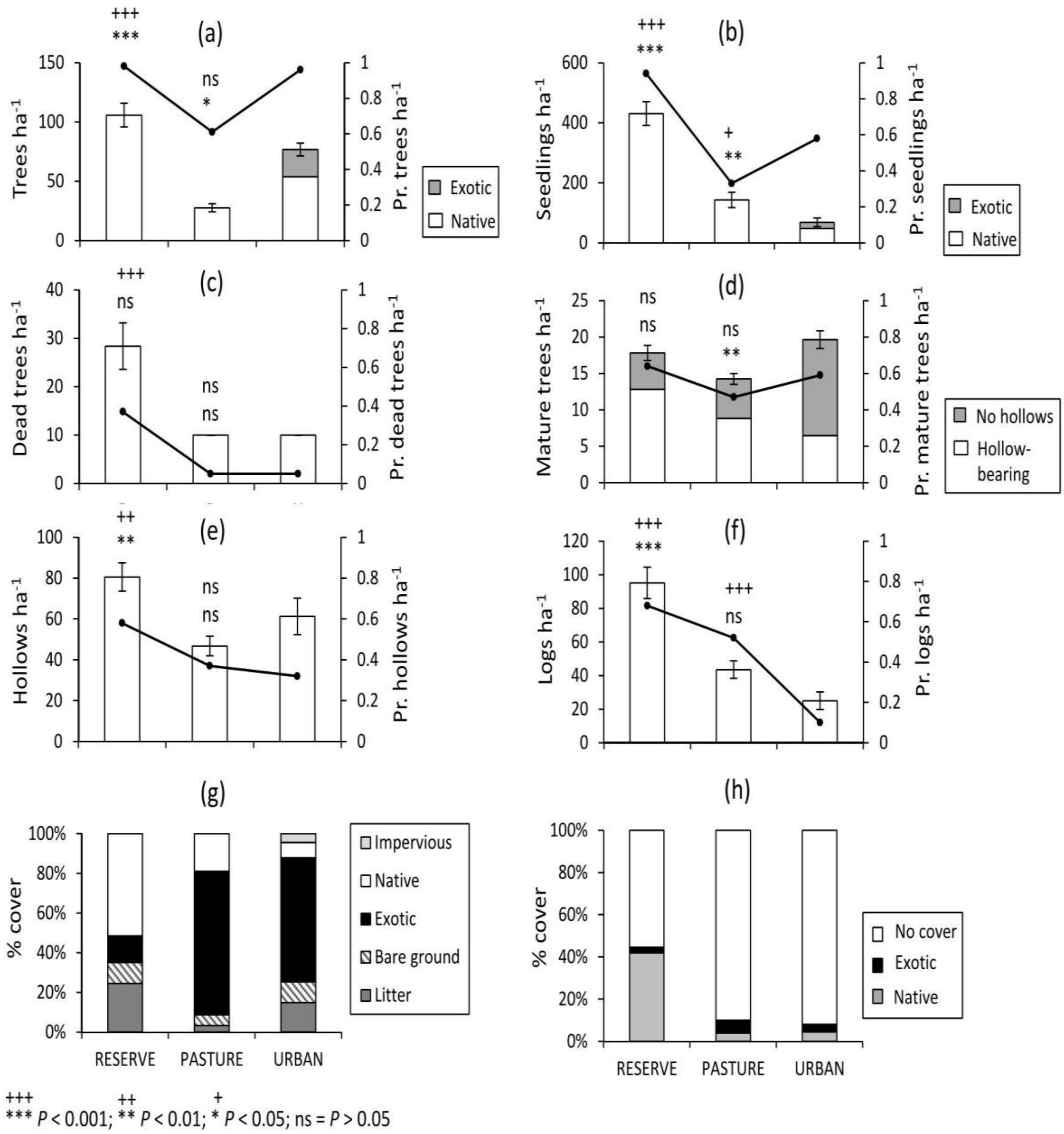

Figure 2. The average density (± standard error) of each measured habitat structure when detected (bars; left y-axes) with super-imposed probabilities of occurrence (solid lines; right y-axes) for reserves, pasture and urban greenspace. Habitat structures include (a) all trees (native and exotic), (b) seedlings, (c) dead trees, (d) mature trees (hollow-bearing and no hollows), (e) hollows, and (f) logs, as well as the (g) percentage groundcover, and (h) percentage mid-storey cover. Symbols above figures a-f show the degree of significant difference between the urban greenspace and semi-natural reserves and agricultural land. Statistical differences are based on zero-inflated count (i.e. density of habitat structures when detected; denoted by symbol *****) and binary models (i.e. probability of habitat structure occurrence; denoted by symbol **+**).

Dead trees

The density of dead trees, when encountered, in urban greenspace and pasture was not significantly different ($P = 0.671$) from the density recorded in reserves (Figure 2c). However, on average, the density of dead trees per hectare was 21 times higher in reserves compared with urban greenspace and pasture. The probability of dead tree occurrence in urban greenspace was significantly lower ($P < 0.0001$) than in reserves. There was no difference in the density ($P = 1.000$) or the probability of occurrence ($P = 0.672$) of dead trees between urban greenspace and pasture. Five dead trees were recorded in pasture and urban greenspace compared with 105 dead trees in reserves. The proportion of trees > 10 cm DBH that were dead was higher for pasture (5%) compared with urban greenspace (1%).

Mature trees

The density ($P = 0.278$) and the probability of occurrence ($P = 0.461$) of mature trees did not differ significantly between urban greenspace and reserves (Figure 2d). There also was no significant difference ($P = 0.08$) between the probability of occurrence of mature tree in urban greenspace and pasture. However, the density of mature trees was significantly higher ($P < 0.001$) in urban greenspace than in pasture.

Hollow-bearing trees

There was no significant difference ($P = 0.185$) in the density of hollow-bearing trees between urban greenspace and reserves. However, the probability of occurrence of hollow-bearing trees was significantly lower ($P < 0.001$) in urban greenspace than in reserves. In contrast, the density of hollow-bearing trees was significantly higher ($P < 0.001$) in urban greenspace than in pasture, but the probability of occurrence of hollow-bearing trees was not significantly different ($P = 0.536$) between these land-use types. The percentage of mature trees that were hollow-bearing was high for reserves (72%) and pasture (63%), but not for mature trees in urban greenspace (33%). We recorded no exotic trees with hollows.

Hollows

The density and probability of occurrence of hollows was significantly lower ($P < 0.001$) in urban greenspace compared with reserves (Figure 2e). However, there was no significant difference in the density ($P = 0.062$) or probability of occurrence ($P = 0.441$) of hollows between urban greenspace and pasture. When separated by entrance size, large hollows (>10 cm) were approximately 3.5 times more abundant in reserves than in urban greenspace and pasture. On average, each hollow-bearing tree supported 3.2, 3.8, and 4.4 hollows in urban greenspace, pasture and reserves, respectively.

Logs

The density and probability of occurrence of logs was significantly lower ($P < 0.\ 0001$) in urban greenspace than in reserves (Figure 2f). Similarly, the probability of occurrence of logs was significantly lower ($P < 0.0001$) in urban greenspace than in pasture. However, we recorded no significant difference ($P = 0.149$) in the density of logs between urban greenspace and pasture. On average, the volume of wood calculated from logs in urban greenspace was 0.3 m^3 ha^{-1} compared with 1.8 m^3 ha^{-1} and 4.8 m^3 ha^{-1} in pasture and reserves, respectively.

Ground and mid-storey cover

Exotic groundcover was significantly ($P < 0.001$) higher in urban greenspace (63%) and pasture (72%) compared with reserves (13%; Figure 2g). Conversely, groundcover in reserves was dominated by native vegetation (51%) and litter (24%), which were significantly lower ($P < 0.001$) in urban greenspace and pasture. Native shrub species were prevalent (42%) in the mid-storey of reserves but significantly lacking ($P < 0.001$) in urban greenspace (8%) and pasture (10%; Fig. 2h).

Discussion

In this study we asked: What is the availability of habitat structures in urban landscapes and how does this compare with agricultural land and semi-natural reserves? To the best of our collective knowledge, ours is one of the first studies to explicitly quantify the relative availability of multiple habitat structures in urban landscapes and directly compare this with other dominant land-use types. Overall, our findings confirm that urban landscapes support greatly diminished habitat structures important for biodiversity. Assuming that this problem is replicated in cities around the world, our study has worldwide implications for the current management of habitat structures in urban landscapes. Reductions in the availability of critical, life-supporting habitat structures jeopardises the ecological sustainability of urban landscapes (e.g. Di Giulio, Holderegger, & Tobias, 2009). In contrast, a multitude of species groups stand to benefit from improvements to the management of habitat structures in urban landscapes, including plants, mammals, birds, reptiles, amphibians, invertebrates and microorganisms (e.g. McDonald, Kareiva, & Forman, 2008; McKinney, 2008; Stagoll, Lindenmayer, Knight, Fischer, & Manning, 2012).

Reduced availability of habitat structures

The density and/or probability of occurrence of habitat structures (except mature trees) in our study area were significantly lower in urban greenspace compared with reserves. Urban resource limitations in our study area were comparable with agricultural land, where declines in habitat structures (e.g. young trees and logs) have profound consequences for biodiversity (e.g. Gibbons et al., 2008b; Hanspach et al., 2012). Addressing this problem in urban environments warrants immediate attention given the unprecedented rate of global urban expansion (UNDP, 2011). This requires a re-think of how habitat structures are currently managed in urban settings.

We found that although significantly fewer trees occur in urban greenspace compared with reserves, the availability of mature trees did not differ between these land-use types. The availability of mature trees also was higher in urban greenspace than in pasture. These results indicate that there are potentially better outcomes for mature tree-dependant fauna in urban landscapes compared with pasture (e.g. Stagoll et al., 2012b). However, fragmented urban landscapes may pose other threats to tree-dependant species (e.g. road mortality; Dique et al., 2003). Legislation protecting mature trees in Canberra's urban environment (Tree Protection Act, 2005) is likely responsible for reserve-like mature tree densities, which, in turn, underscores the importance of implementing targeted protection policies for individual habitat structures in cities. Nevertheless, structures typically associated with mature trees, including hollows and large quantities of logs and litter, are significantly reduced in urban greenspace. Compared with reserves, we observed a reduced proportion of hollow-bearing trees, hollows per tree, and hollows with larger entrance sizes in urban greenspace. This suggests that hollow-dependant fauna, especially species that require large hollows for nesting (e.g. large birds, marsupials), may be particularly disadvantaged in urban landscapes.

Tree regeneration is especially limited in the urban landscape we studied. This is likely because: (1) significantly fewer seedlings were recorded in the urban greenspace compared with both reserves and pasture; and (2) efforts to protect young trees were rarely observed. This result is consistent with other cities globally (e.g. Bangalore, India; Nagendra and Gopal, 2010). Natural tree regeneration is especially hindered in urban greenspace due to impervious surfaces and the spread of weeds that dominate the ground layer (e.g. Stinson et al., 2006). This means that active management strategies that encourage tree regeneration and the maintenance of healthy tree age structures are needed, including widespread re-plantings and installing protective structures to aid tree growth or regrowth. For example, in Hong Kong, China using tree guards and weed mats to protect seedlings can increase the establishment, survivorship and growth of trees (Lai & Wong, 2005). These strategies are vital if habitat structures that form over extended time periods such as mature trees, hollows and logs are to be retained in perpetuity for future generations (e.g. Vesk et al., 2008; Lindenmayer et al., 2013).

Conflicts between public safety and retention of urban habitat structures

Conflicts between public safety and retention of certain habitat structures in urban greenspace likely explains why hollows, dead trees, fallen debris and mid-storey vegetation are reduced and in some cases (e.g. logs) almost entirely absent from the urban landscape. In cities, human interests and safety concerns tend to take precedent over concerns for biodiversity and this is reflected in policies that underpin the intentional removal of habitat structures perceived as hazardous to humans. For example, tree maintenance policies on public land in Canberra aim to remove dead trees and prune hollow branches as these structures pose safety risks to people and property (ACT Government, 2013). However, tidy-up practices that reduce structures considered hazardous to humans occur to the detriment of biodiversity that is supported by these same structures (McDonnell, 2007). For example, Carpaneto et al. (2010) found that hollow-bearing trees in parks in Rome support threatened saproxylic beetles, yet 41% of habitat trees were listed as dangerous and identified for removal.

Our results indicate that logs and mid-storey vegetation are especially limited in urban greenspace. The removal of woody debris and shrubs from urban areas is likely driven by public perceptions that these structures are fuel for wildfires. However, evidence suggests that house loss from wildfires occurs almost exclusively within close proximity to the wildland-urban interface (Chen and McAneney, 2004; Gibbons et al., 2012). There is also evidence that intensive local-scale fuel reduction close to properties most at risk to wildfire (e.g. houses along urban fringes) are likely to be more effective at mitigating the impacts of wildfire than widespread fuel reduction strategies (e.g. Gibbons et al., 2012). This means that retaining logs, litter and mid-storey vegetation within the majority of urban greenspace, which is away from the urban fringe, is unlikely to increase the risk to built assets or people from wildfire. Overgrown vegetation also may appear unkept and increase people’s fear of crime and wildlife perceived as dangerous (e.g. snakes). Collectively, these factors have resulted in highly manicured greenspaces with reduced complexity dominating urban landscapes (e.g. Bjerke et al., 2006). Yet, complexity in vegetation structure and groundcover is vital for wildlife as it provides shelter, connectivity and foraging opportunities (e.g. Brearley et al., 2010).

Towards improved management of urban habitat structures

Urban landscapes must be managed in a holistic manner to achieve conservation and socio-economic goals. This requires collaboration between conservationists, practitioners (e.g. architects, developers, arborists) and urban residents so that multi-functional urban greenspaces can be established. We encourage policymakers to consider the important biodiversity values of habitat structures in urban landscapes by formulating protection policies that enable authorities to mandate on-the-ground conservation actions (see also Stagoll et al., 2012b; Lindenmayer et al., 2013). We anticipate that strategies that encourage the maintenance and perpetuation of urban habitat structures will not only benefit biodiversity but also improve key ecological processes (e.g. nutrients turnover, and groundwater saturation) and provide financial and community rewards. For example, using logs, woodchips and native shrubs as part of urban design features can reduce the costs of lawn maintenance (e.g. mowing, weeding; Henderson et al., 1998). Similarly, large trees are important to wildlife but they also have aesthetic, cultural and functional roles (e.g. providing shade, increasing real estate value; e.g. Thaiutsa et al., 2008; Ishii et al., 2010).

We propose three guiding strategies that integrate socio-economic priorities and biodiversity conservation, which can be incorporated into the design, landscaping and management of urban landscapes to better maintain habitat structures.

1. Establish conservation reserves

The availability of all habitat structures measured in our study was greatest in reserves. Retrospectively or prospectively setting aside conservation-specific land within and adjacent to cities is an important step towards conserving biodiversity because reserves can ‘bridge’ urban resource gaps at a landscape scale by providing an alternative source of habitat to built-up urban areas. Reserves also offer refuge to urban-sensitive species (e.g. Catterall et al., 1998) and opportunities for the public to experience nature (e.g. Chiesura, 2004).

2. Spatial zoning of habitat structures within urban areas to reduce risk

Conflicts between biodiversity conservation and public interest or safety can be addressed through strategic zoning of hazardous habitat structures so that these are retained instead of removed (Figure 3a-c). Landscaping techniques can separate public facilities like playgrounds and walkways from structures that pose a risk (e.g. dead trees; Stagoll et al., 2012b). Segregating the public from areas of re-growth / re-planting is also a useful technique to protect young trees and limit the spread of weeds. In urban landscapes, habitat structures need to be managed even at the level of the stem, log and hollow-bearing branch because of the reduced availability of these structures and the situation-specific ways of overcoming conflicts of interest (Lindenmayer et al., 2013).

Figure 3. Example management strategies for habitat structures: (a) mature native tree retained along a roadside margin adjacent to residential housing; (b) dead hollow-bearing tree retained by establishing a 'safe zone' with wooden posts and native understorey shrubs; (c) fallen log retained in an urban park; (d) simple signage to raise community awareness of the biodiversity value of retained woody debris in public areas.

3. Engage residents in conservation practice

Implementation of the two above-mentioned strategies requires education and participation of urban residents (Figure 3d). The composition of urban greenspace and the persistence of certain habitat structures will depend on people's perceived values of these structures (Groves et al., 2002). For example, changes in public attitudes towards the important value of native habitat are largely responsible for an increase in the percentage of indigenous trees planted in Christchurch, New Zealand (Stewart, Ignatieva, & Meurk, 2004). Overall, a deeper understanding of biodiversity and sustainability issues is needed to raise awareness, encourage tolerance, and dispel misconceptions related to certain habitat structures (McKinney, 2002; McDonnell, 2007).

Conclusion

Habitat structures important for biodiversity are significantly reduced in urban greenspace compared with semi-natural reserves. Urban resource limitations are comparable with highly altered agricultural land, which is a concern demanding attention as global urbanisation intensifies. Improved protection policies, management strategies, and on-the-ground conservation actions are needed to address current urban resource deficiencies. Establishing conservation reserves, spatial zoning of habitat structures deemed hazardous to humans in existing urban greenspace, and engaging city residents in local conservation efforts are three practical strategies that can be implemented at multiple spatial scales to maintain and perpetuate habitat structures in urban landscapes worldwide. This is vital for biodiversity and the well-being of human populations in urban areas.

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Supporting information

Table S1. Summary of habitat structures measured, the sampling methods used, and the species groups (biodiversity) that may benefit from an increased availability of habitat structures in urban landscapes.

Response variable	**Sampling method**	**Species groups**
Count of trees	All living and dead native and exotic stems with a diameter at breast height over bark (1.3m; DBH) of > 10 cm were identified to species level using regional guides (Eddy et al. 2011; Edwards 1979; National Parks Association 2007). The DBH of the largest stem for multi-stemmed trees was measured (Gibbons et al. 2008).	Tree dependant fauna including microbes, invertebrates, reptiles, birds, bats and arboreal mammals.
Count of seedlings	All living native and exotic seedlings / saplings with a DBH of ≤ 10 cm were counted.	As above
Count of mature trees, hollow-bearing trees and hollows	We considered trees ≥ 50 cm DBH as mature, because trees larger than this are formally protected in Canberra (ACT Government 2005). All trees were inspected for hollows from all angles on the ground by the same observer using binoculars (Rayner et al. 2011). Hollows with entrance sizes ≥ 2cm were counted and allocated to three size classes: 2-5, 6-10, >10 cm.	Mature tree and hollow-dependant flora and fauna including epiphytes, invertebrates, reptiles, birds, bats and arboreal mammals.
Count of logs	All fallen woody debris ≥ 1 m in length with a diameter of ≥ 10 cm was counted (Manning et al. 2007). The length (L) and estimated average diameter (D) was measured and volumes calculated using the formula $L \times \pi (D / 2)^2$.	Microbes, invertebrates, reptiles and terrestrial mammals.
Proportion of ground (< 1 m) and mid-storey (1-4 m) cover	Using an intercept method (adapted from McDonald et al. 1990) we randomly selected a point along the 20 m axis of each plot and walked a 50 m transect where every 2 m (25 points) the dominant ground and mid-storey cover was selected from several possible categories. Ground cover categories included: impervious surface, native or exotic vegetation (e.g. grasses, forbs, sedges), bare ground, or litter (leaves, bark, woody pieces < 1 m in length with diameters <	Microbes, invertebrates, reptiles and terrestrial mammals.

	10 cm). Mid-storey categories included: no cover, native or exotic vegetation (shrubs, flowering understorey trees).

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Table S2. Summary analyses for zero-inflated conditional models with best fit truncated Poisson or truncated negative binomial (NB) distributions and logistic regression models for ground and mid-storey cover. Significant effects are presented as Chi-squared statistics (degrees of freedom) with corresponding probabilities. Bold probabilities represent habitat structures for which land-use has a significant effect in terms of the probability of occurrence (binary model) and conditional density (count model) of each structure.

Discrete variables	**Model Distribution**	**Model residual deviance**		**Fixed effect of land use**			
		Binary (293 d.f.)	*Count*	*Binary (4 d.f.)*		*Count (4 d.f.)*	
All trees	NB	177.6	286.7 on 247 d.f.	69	***P* < 0.001**	4.8	*P* = 0.308
Native trees	NB	233.9	274.5 on 236 d.f.	51.6	***P* < 0.001**	0.1	*P* = 0.998
Seedlings	NB	302.7	231.0 on 177 d.f.	92.7	***P* < 0.001**	6	*P* = 0.199
Dead trees	Poisson	201.2	125.3 on 40 d.f.	51	***P* < 0.001**	53.6	***P* < 0.001**
Mature trees	Poisson	394.8	204.9 on 163 d.f.	6.4	*P* = 0.171	19.2	***P* < 0.001**
Hollow-bearing trees	Poisson	373.2	104.3 on 118 d.f.	17	***P* < 0.01**	32.4	***P* < 0.001**
Hollows	NB	374.3	138.2 on 119 d.f.	16.6	***P* < 0.01**	0.4	*P* = 0.983
Fallen logs	NB	307.6	152.7 on 126 d.f.	94.3	***P* < 0.001**	2.6	*P* = 0.626
Categorical variables		*Binary (293 d.f.)*	-	*Binary (2 d.f.)*		-	
G_impervious	Binomial	301.1	-	251.1	***P* < 0.001**	-	
G_native	Binomial	2852	-	1348	***P* < 0.001**	-	
G_exotic	Binomial	3382	-	2215	***P* < 0.001**	-	

G_bare	Binomial	1156	-	58	***P* < 0.001**	-
G_litter	Binomial	1724	-	522	***P* < 0.001**	-
M_no cover	Binomial	3161	-	1243	***P* < 0.001**	-
M_exotic	Binomial	1332	-	42	***P* < 0.001**	-
M_native	Binomial	2446	-	1700	***P* < 0.001**	-

Table S3. List of living native and exotic tree species recorded in our study area (alphabetically ordered). The total number of trees (stems > 10 cm DBH), seedlings (stems ≤ 10 cm DBH), and hollow-bearing trees are provided for reserves, pasture and the urban greenspace.

Species	**Common name**	**Total trees**			**Total seedlings**			**Total hollow-bearing trees**		
		Reserve	***Pasture***	***Urban***	***Reserve***	***Pasture***	***Urban***	***Reserve***	***Pasture***	***Urban***
Natives (16 sp.)										
Eucalyptus blakelyi	Blakely's red gum	1808	243	199	1596	196	89	34	15	23
E. bridgesiana	Apple box	375	41	36	244	22	16	8	6	0
E. dalrympleana	Mountain gum	2	0	10	1	0	1	0	0	0
E. delegatensis	Alpine ash	0	0	1	0	0	0	0	0	0
E. dives	Broad-leaved peppermint	20	1	20	17	0	1	1	0	1
E. fastigata	Brown barrel	0	0	5	0	0	0	0	0	0
E. goniocalyx	Bundy	1	0	5	0	0	1	0	0	0
E. macrorhyncha	Red stringybark	130	5	16	62	0	0	3	4	7
E. mannifera	Brittle gum	8	0	127	5	0	19	2	0	2
E. melliodora	Yellow box	1241	173	173	952	131	69	27	12	18
E. nortonii	Mealy bundy	2	0	6	2	0	2	0	0	0
E. polyanthemos	Red box	120	12	19	72	4	1	2	2	0
E. rossii	Scribbly gum	272	100	50	201	79	38	10	2	1
E. rubida	Candlebark	0	0	21	0	0	9	0	0	0
E. sideroxylon	Red ironbark	0	0	25	0	0	1	0	0	0
E. viminalis	Ribbon gum	0	0	38	0	0	4	0	0	0
Exotics (21 sp.)										
Acer pseudoplatanus	Sycamore maple	0	0	14	0	0	5	0	0	0
Betula pendula	Silver birch	0	0	43	0	0	9	0	0	0
Cedrus atlantica	Atlas cedar	0	0	6	0	0	0	0	0	0
Cupressus sempervirens	Mediterranean cypress	0	0	6	0	0	0	0	0	0
Fraxinus exelsior	Common ash	0	0	20	0	0	11	0	0	0
Fraxinus ornus	Flowering ash	0	0	7	0	0	6	0	0	0

Liquidamber styraciflua	American sweetgum	0	0	8	0	0	1	0	0	0
Pinus elliottii	Sawn pine	0	0	4	0	0	0	0	0	0
Pinus radiata	Monterey pine	0	0	47	0	0	3	0	0	0
Pistacia chinensis	Chinese pistachio	0	0	11	0	0	7	0	0	0
Platanus acerifolia	London plane	0	0	5	0	0	1	0	0	0
Populus deltoides	Eastern poplar	0	0	20	0	0	11	0	0	0
Populus nigra	Black poplar	0	0	12	0	0	0	0	0	0
Prunus cerasifera nigra	Purple-leaved Cherry-plum	0	0	25	0	0	23	0	0	0
Quercus borealis	Red oak	0	0	47	0	0	9	0	0	0
Salix alba vitellina	Golden willow	0	0	1	0	0	0	0	0	0
Sequoia giganteum	Giant sequoia	0	0	2	0	0	0	0	0	0
Sophora japonica	Japanese pagoda	0	0	13	0	0	13	0	0	0
Ulmus americana	American elm	0	0	3	0	0	1	0	0	0
Ulmus glabra	Wych elm	0	0	2	0	0	0	0	0	0
Grand total	**37 species**	**3979**	**575**	**1048**	**3152**	**432**	**351**	**87**	**41**	**52**

Paper II. The future of large old trees in urban landscapes

In Paper I, I showed that many important habitat structures are reduced in urban landscapes, including hollow-bearing trees. In Paper II, I used a dynamic simulation model to predict the future availability of hollow-bearing trees in the urban landscape. I also tested the efficacy of alternative tree management strategies that could improve long term trajectories for large tree populations in urban landscapes.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2014). The future of large old trees in urban landscapes. *PLoS One*, 9(6), e99403, 1-11.

Abstract

Large old trees are disproportionate providers of structural elements (e.g. hollows, coarse woody debris), which are crucial habitat resources for many species. The decline of large old trees in modified landscapes is of global conservation concern. Once large old trees are removed, they are difficult to replace in the short term due to typically prolonged time periods needed for trees to mature (i.e. centuries). Few studies have investigated the decline of large old trees in urban landscapes. Using a simulation model, we predicted the future availability of native hollow-bearing trees (a surrogate for large old trees) in an expanding city in southeastern Australia. In urban greenspace, we predicted that the number of hollow-bearing trees is likely to decline by 87% over 300 years under existing management practices. Under a worst case scenario, hollow-bearing trees may be completely lost within 115 years. Conversely, we predicted that the number of hollow-bearing trees will likely remain stable in semi-natural nature reserves. Sensitivity analysis revealed that the number of hollow-bearing trees perpetuated in urban greenspace over the long term is most sensitive to the: (1) maximum standing life of trees; (2) number of regenerating seedlings ha^{-1}; and (3) rate of hollow formation. We tested the efficacy of alternative urban management strategies and found that the only way to arrest the decline of large old trees requires a collective management strategy that ensures: (1) trees remain standing for at least 40% longer than currently tolerated lifespans; (2) the number of seedlings established is increased by at least 60%; and (3) the formation of habitat structures provided by large old trees is accelerated by at least 30% (e.g. artificial structures) to compensate for short term deficits in habitat resources. Immediate implementation of these recommendations is needed to avert long term risk to urban biodiversity.

Keywords: biodiversity, biodiversity offsets, lag effects, simulation modelling, tree hollow, tree mortality, tree regeneration, urban greenspace, urban tree management

Introduction

Large old trees have been defined as keystone ecological structures because, relative to their size, they are disproportionate providers of resources crucial to other species [1, 2]. As trees mature, they begin to form a set of unique physical attributes or structural elements, including large volumes of coarse woody debris and litter, peeling bark, dead branches and hollows [3, 4]. Habitat structures provided by large old trees take centuries to form and are typically not provided by younger trees [e.g. 5]. For example, hollows in *Eucalyptus* typically begin to form in trees 120-220 years old [6]. Hollows alone provide critical nesting resources for a diverse range of taxa worldwide, including invertebrates [e.g. 7], reptiles [e.g. 8], birds [e.g. 9], and mammals [e.g. 10].

Once large old trees are removed, they can be extremely difficult to replace in the short term because of the prolonged time period needed for trees to mature. This time lag can have serious ecological and management implications, particularly in modified landscapes where the rate of large old tree removal exceeds the rate of tree replacement [e.g. 11, 12-14]. Species that depend on large old trees for survival (e.g. hollow-dependent fauna) may face extinction in the short term without actions that reverse current patterns of tree decline [see 2 for a discussion].

Human activities such as land clearance, logging and livestock grazing are responsible for the decline of large old trees in a diverse range of ecosystems, including: conifer forests in Europe [e.g. 15] and North America [e.g. 16], tropical rainforest in South America [e.g. 17], and agricultural land in Australia [e.g. 18]. However, few studies have investigated the decline of large old trees in urban landscapes [e.g. 19, 20]. This is a major concern given the unprecedented rate of global urbanisation, one of the most rapid and destructive forms of land-use change [e.g. 21, 22]. Population growth and rising demand for urban living space invariably puts pressure on existing urban habitat that can be important for biodiversity [e.g. 23, 24, 25]. However, a great deal of uncertainty remains about the future of habitat structures in urban landscapes, especially structures like large old trees that are known to limit some species [e.g. 26, 27]. Large old trees are especially vulnerable to removal in urban landscapes worldwide, due to the potential safety risks posed to the public and infrastructure [e.g. falling branches; 20, 28, 29]. Therefore, obtaining information about the future availability of large old trees in urban landscapes is of high priority, especially for practitioners who are challenged by balancing urban growth and maintaining critical habitat for biodiversity over the long term.

Although there are parallels between urban landscapes and other modified environments (e.g. agricultural land), the management of trees in human-dominated urban settings poses a suite of unique and complex challenges. The key interacting drivers of tree loss in the urban matrix include: (1) urban sprawl and in-fill practices [e.g. 30], (2) public safety policies that facilitate managed tree removal in existing greenspace to protect people and infrastructure [e.g. 20], and (3) reduced tree regeneration [e.g. 31]. Despite these challenges, urban environments also provide opportunities for innovative tree management, community engagement, people-led conservation strategies, and biodiversity offsets [e.g. public tree planting initiatives and artificial nest box projects; 32].

In this study, we used a simulation model to predict the future availability of native hollow-bearing trees in a rapidly expanding urban landscape. We used hollow-bearing trees as a surrogate for large old trees and associated habitat structures [e.g. coarse woody debris, peeling bark; 4, 33, 34]. This is because it is well established that as trees age and their size increases so too does the probability of hollow occurrence [e.g. 5, 35, 36]. Our four main study objectives were to: (1) compare future trajectories in hollow-bearing trees in urban greenspace with semi-natural nature reserves under existing land management practices; (2) identify which variables can be manipulated to increase the number of hollow-bearing trees occurring in urban greenspace over the long term; (3) test the efficacy of multiple alternative tree management strategies aimed at mitigating the decline of hollow-bearing trees; and (4) formulate recommendations that can be widely applied by practitioners to better maintain and perpetuate large old trees and their associated habitat structures in urban landscapes. Given the widespread nature of this issue in urban landscapes, we anticipate that our findings will be relevant to urban practitioners globally.

Materials and Methods

Ethics statement

This research was conducted under ethical approval (protocol number A2012 / 37; The Australian National University Ethics Committee). Vegetation surveys undertaken on nature reserves and public greenspace were approved by permit from the ACT Government, Territory and Municipal Services in compliance with the Nature Conservation Act 1980. Field studies did not involve endangered or protected species.

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 Australia’s eighth largest city covering an area of 810 km^2. The city supports a population of 375,000 people, which is projected to double by 2056 [37]. Canberra is a highly planned city described as the “Bush Capital” because of the extensive suburban tree cover and 34 nature reserves flanking the urban boundary [38]. The city is situated in the ecologically diverse Southern Tablelands region west of the Great Dividing Range. Lowland box-gum *Eucalyptus* woodlands and grasslands once dominated the region [39]. Box-gum grassy woodlands are characterised by two dominant species, yellow box (*Eucalyptus melliodora*) and Blakely’s red gum (*E. blakelyi*) that occur in association with other eucalypt species, including apple box (*E. bridgesiana*), red box (*E. polyanthemos*), red stringybark (*E. macrorhyncha*), and scribbly gum (*E. rossii*). Extensive land clearance for stock grazing and urban development has led to a near 95% decline in intact box-gum grassy woodlands, which is now listed as a critically endangered ecological community [40]. What vegetation remains exists in semi-natural nature reserves or as highly modified isolated remnant patches and scattered paddock and urban trees [e.g. 41, 42].

Sampling design

We confined our sampling effort to a single vegetation type: the predicted pre-European (pre-1750) extent of box-gum grassy woodland. Within this vegetation type, we stratified sampling according to two dominant land-use types and five geographic zones, creating a total of 10 strata. Our land-use types were: (1) nature reserves, which are designated semi-natural areas managed for conservation; and (2) urban greenspace, made up of publicly accessible parklands (60%), roadside margins (24%), remnant vegetation (9%), and sports grounds (7%). Urban greenspace accounted for 11% of the total urban environment in our study area. We divided our study landscape into five geographic zones to capture variability and avoid biasing sampling effort to areas with specific local or historical attributes (e.g. fire history). An equal number of fixed area plots (50 x 20 m; 0.1 ha) were randomly allocated by land-use type (n = 100) and geographic zone (n = 40). This resulted in a total of 200 plots or 20 ha of sampled land from 28 reserves and 100 urban greenspaces. Plots were > 250 m apart to minimise spatial dependence and allocated to greenspace ≥ 0.2 ha.

Data collection

We measured the diameter at breast height over bark (DBH; 1.3 m above ground) of every living and dead tree in each plot. We measured only the largest stem of multi-stemmed trees [43]. Trees with stems < 1.3 m above the ground were measured at the base of the stem. The number of naturally regenerating and planted seedlings ≤ 10 cm (DBH) were counted in each plot and formed the first size class of our tree population. We identified all living trees to species level. Each tree was inspected for hollows from all angles on the ground using binoculars (10 x 25). One observer (DSL) completed this task to reduce multi-observer bias and maintain consistency in hollow identification [44]. Our objective was not to determine the absolute number of hollows but rather relative hollow occurrence per tree. We selected a minimum entrance size of 2 cm for hollows. This was because: (1) the full range of hollow-dependent vertebrate taxa, including marsupials, birds, and bats, would be accounted for; and (2) hollows smaller than 2 cm were difficult to reliably identify from the ground [45].

Simulation model

The simulation model described in [12], tracks the mean DBH of trees, including hollow-bearing trees, in separate size cohorts over time. The model has pre-defined rates of tree mortality and recruitment applied at each time step. For this study, we ran separate simulations for native tree populations occurring in nature reserves and urban greenspace. Exotic trees were recorded only in the urban greenspace and accounted for 30% of all recorded trees. We excluded exotic trees from our analyses because only native trees were recorded with hollows in our study area. Simulation models for both land-use types were parameterised with the following baseline data: the current number of native trees in existing stands sorted by DBH cohort; the predicted age and growth rate of trees; the frequency of regeneration events; the number of seedlings at each regeneration event; and the rate of tree mortality.

There were five principle steps in our modelling process (summarised in Figure 1 and described further in Summary S1):

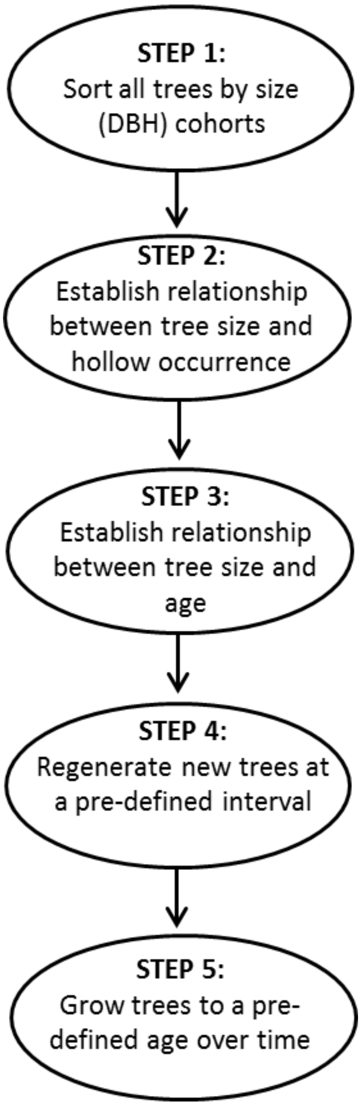

Figure 1. Simple schematic highlighting the five principle steps of our simulation model.

(1) We calculated the mean number of trees in 10 cm DBH size cohorts (ranging from 0.1-10 cm to > 100 cm) for each native tree species and dead trees, using data collected in each land-use type (Table S1).

(2) We used a generalised logistic regression model with a binomial distribution and logit link to establish a relationship between hollow occurrence (i.e. the presence of at least one hollow ≥ 2 cm; binary response) and tree size (i.e. DBH; explanatory variable). We also fitted tree species as an explanatory variable in our model. Based on correlations in hollow occurrence by DBH between individual species, we identified three distinct species groupings. Species group one included yellow box, apple box, brittle gum (*E. mannifera*), broad-leaved peppermint (*E. dives*), bundy (*E. goniocalyx*), mealy bundy (*E. nortonii*), brown barrel (*E. fastigata*), alpine ash (*E. delegatensis*), ribbon gum (*E. viminalis*), mountain gum (*E. dalrympleana*), candlebark (*E. rubida*) and ironbark (*E. sideroxylon*). Group two included Blakely's red gum, red box, red stringybark and scribbly gum. Group three was dead trees. We found that species groups differed significantly (Wald statistic = 101.5; $P < 0.001$) from each other (Table 1). The relationship between tree size and hollow presence was highly significant in our model (Wald statistic = 388.1; $P < 0.001$). The area under the receiver operating characteristic curve of our model was 0.92, indicating that the discriminating ability of our model was excellent [46]. For each species group, we derived separate model equations which took the form:

$$\textit{Logit (Pr. Hollows)} = -7.112 + (0.086 \times \text{DBH}) + (\text{species group estimate})$$

(3) We established a relationship between DBH and tree age using the following equation:

$$\text{Age} = 0.02 \times \pi \times (\text{DBH}_{\text{standardised}} / 2)^2$$

where $\text{DBH}_{\text{standardised}}$ is the yellow box equivalent diameter for each tree. Yellow box is the only tree species for which data exist to establish a relationship between age and DBH [47]. We scaled all DBH values for each tree species relative to that of a yellow box equivalent using the method described in [18, 26].

Table 1. Generalised logistic regression model used to predict the proportion of hollow-bearing trees in each 10 cm DBH (diameter at breast height) cohort. Coefficients, standard errors, 95% confidence intervals, and *P*-values are presented with species group one held as the reference level.

Variables	**Coefficient**	**Standard error**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	***P*-value**
Intercept	-7.112	0.335	-7.769	-6.456	< 0.001
Species group 1	0.000	-	-	-	-
Species group 2	1.413	0.274	0.876	1.949	< 0.001
Species group 3	3.861	0.383	3.110	4.613	< 0.001
DBH	0.086	0.004	0.077	0.095	< 0.001

To do this, we first calculated each DBH value as a proportion of the maximum DBH recorded for each tree species and then multiplied this value by the largest DBH recorded for yellow box in our study area (151cm). Therefore, we assumed that all species had proportionally equal growth rates that were similar to that of yellow box. Although this approach is not ideal because it is unlikely to yield precise age estimates for each species, it currently is the most practicable solution available in the absence of age-DBH relationship data for other eucalypt species [26, 48]. Therefore, our model had a degree of uncertainty related to tree growth rates, as these data likely differ for each species. However, a previous study [12] found that long-term predictions for mature trees is not sensitive to uncertainty in this variable and suggests that the focus should instead be on testing the effects of uncertainty for other parameters in the model.

(4) We simulated tree regeneration in both land-use types to ensure that uncertainties associated with regeneration were reflected in our models. Tree regeneration is an event-driven process that can be sporadic and influenced by natural phenomena and/or anthropogenic factors such as climate, competition, and planting effort [e.g. 31, 49]. At each regeneration event, viable seedlings may or may not establish and survive over time. To simulate these uncertainties, the number of seedlings ha^{-1} for each run of our model was drawn randomly from a Poisson distribution with the mean equal to the mean number of trees recorded in the 0-10 cm DBH cohort for each species group. For species group one and two in urban greenspace, the mean

number of trees in the 0-10 cm DBH cohort was 11 and 13 seedlings ha^{-1}, respectively. For species group one and two in nature reserves, the mean number of trees in the 0-10 cm DBH cohort was 119 and 193 seedlings ha^{-1}, respectively. The time-step for each run of the model was equivalent to the average age of trees in the 0-10 cm DBH cohort for both land-use types, which was approximately 8 years.

(5) Annual tree mortality was modelled in a density-dependent manner to reflect declines in the number of trees over successive DBH cohorts or as trees age. Therefore, we assumed that tree densities would naturally thin out over time due to factors such as competition among conspecifics [50]. To simulate this process, we calculated annual mortality for each DBH cohort using the equation:

$$1 - s^{(1/y)}$$

where s is the proportion of trees that survive from one cohort to the next, and y is the number of years it takes trees to progress from one cohort to the next by 10 cm DBH increments. However, in some urban greenspaces (e.g. roadside margins), density-dependent mortality may be less pronounced as tree survivability may instead be predominantly influenced by tree planting and protection efforts. Therefore, for urban greenspace, we also tested the mean annual mortality rate across all cohorts, which yielded similar model trajectories to density-dependent mortality. We decided to apply density-dependent mortality to both land-use types for consistency and because a majority of urban greenspace sampled constituted parklands and remnant vegetation where natural regeneration and density-dependent mortality may still occur. We set 500 years as the maximum age that living trees will remain standing in both land-use types. This is based on the only longevity estimate available for eucalypts in our study area [47]. It is reasonable to assume that for other eucalypt species this age would also be the upper limit of survivability. Therefore, model uncertainties pertaining to species longevity are likely to be over-estimated and based on a best-case longevity. We assumed that once trees died in urban greenspace, they no longer functioned as hollow-bearing trees into the next time step. This is based on local tree management policies that facilitate dead tree removal on public land [51].

However, for nature reserves, we conservatively estimated that dead trees could remain standing for at least 50 years after initial mortality (i.e. 550 years in total), based on observations of the standing life of dead trees in *Eucalyptus* forests [52], however, we acknowledge the paucity of available data to support this estimate.

The availability of hollow-bearing trees under existing management practices

We used our simulation model, parameterised with those data detailed above, to predict the mean number of hollow-bearing trees ha^{-1} occurring in nature reserves and urban greenspace over time under existing land management protocols. Simulations were undertaken over 300 years using a Monte Carlo simulation based on 300 runs of our model (i.e. the number of iterations required for relatively well-defined distributions). This approach relies on random sampling over multiple simulations to generate probabilities in a heuristic manner [53]. Therefore, for each run of our model, input data for several variables were drawn randomly from defined distributions. The number of recruits was drawn from a Poisson distribution (step 4 above). Annual mortality was drawn from a normal distribution, where negative values were converted to zero. The maximum standing life of living trees was held at 500 years for nature reserves. However, for urban greenspace, values were drawn from a uniform distribution between 60 years (the estimated minimum standing life of trees in our study area) [54] and 500 years (the estimated maximum standing life of trees in our study area). This range of lifespans reflects variation in current tree management practices in different types of urban greenspace. Variables held constant in our model were the period between regeneration events (8 years) and coefficients for the age-DBH (0.019) and DBH-hollow (1.413) relationships (see Table 3 for a summary of parameter values under existing land management protocols).

Variables that can be manipulated to mitigate the decline of hollow-bearing trees

We performed a sensitivity analysis, as described in [55], to identify which variables can be manipulated in urban greenspace to mitigate the decline of hollow-bearing trees. For this analysis, we also used a Monte Carlo simulation based on 300 runs of our model. We repeatedly populated each run of the model with data drawn randomly from uniform distributions for each variable. Where applicable, values were drawn from a wider range than observed under existing management practices to more broadly test a range of alternative management strategies. Variables that can be manipulated by management included: (1) maximum standing life of trees (range: 60-500 years for species groups one and two, based on longevity estimates for urban trees in our study area); (2) number of seedlings ha^{-1} (range: 0-60 seedlings ha^{-1} for species groups one and two, testing various regeneration targets); (3) period between regeneration events (range: 1-50 years, testing various regeneration schedules); (4) rate of annual mortality (range: 0.03-0.1 model coefficients, testing various feasible survivability outcomes); and (5) rate of hollow formation (range: 1.5-3.7 model coefficients, testing a range of hollow acceleration strategies above an observed existing rate (i.e. 1.4) up to a rate observed for dead trees (i.e. 3.8) in our study area, which we assumed indicated a maximal hollow formation rate for living trees). We fixed the coefficient for the DBH-age relationship at 0.019 assuming that this could not be changed appreciably.

We used linear regression to test the relative sensitivity of our response variable (i.e. the mean number of hollow-bearing trees ha^{-1}) against the explanatory variables that are the parameters in our simulation model. We natural log-transformed (ln (x + 1)) our response to satisfy assumptions of normality. There were no significant interactions between explanatory variables and interaction terms were dropped from the final additive model. We used stepwise regression to determine the model of best fit. Percentage variance accounted for by our final model was 40%. Due to the high number of replications used in simulation models, it is inappropriate to rely on conventional *P*-values to indicate statistical significance [56]. Instead, we used relative effect size, as indicated by variance ratios, to identify the most sensitive parameters in our model. Variance ratios were calculated as the mean square of each term change divided by the residual mean squares of the original maximal model (Table 2). Predictions are presented only for variables with the greatest relative effect sizes (i.e. most ecologically important), where all other explanatory variables are held at their mean model values.

Table 2. Linear regression model used to perform a sensitivity analysis of the mean number of hollow-bearing trees ha^{-1} (ln (x + 1) transformed) perpetuated in urban greenspace over 300 years. Means, standard deviations, coefficients, standard errors, and variance ratios, which indicate the relative importance or effect size of each model term, are presented for each explanatory variable used to parameterise our simulation model.

Variables	**Mean**	**Standard deviation**	**Coefficient**	**Standard error**	**Variance ratio**
Intercept	-	-	0.602	0.204	-
Maximum standing life (years)	274.10	88.04	0.004	0.0003	138.61
Number of seedlings ha^{-1}	31.03	12.09	0.009	0.002	13.81
Rate of hollow formation (coefficient)	2.59	0.17	0.151	0.042	11.04
Rate of annual mortality (coefficient)	0.06	0.02	-1.290	1.450	0.31
Period between regeneration (years)	24.74	13.40	0.000	0.002	0.00

Table 3. Summarised values for each variable used to parameterise our simulation model under existing management practices for nature reserves and urban greenspace. Relative values are derived from raw vegetation data or, where applicable, published estimates. Urban management recommendations, derived from a series of simulated alternative management strategies, are indicated for variables identified as being the most ecologically important from a sensitivity analysis.

Variables	**Nature reserves**	**Urban greenspace**	**Urban management recommendations**
Maximum standing life (years)	500	60-500	450 (~40% increase)
Number of seedlings ha^{-1}(all species)	315	25	60 (~60% increase)
Rate of hollow formation	1.4	1.4	2.0 (~30% increase)
Rate of annual mortality	0.03	0.06	-
Period between regeneration (years)	8	8	-

The availability of hollow-bearing trees under alternative management strategies

We also simulated a series of alternative management strategies using our simulation model. We modelled the mean number of hollow-bearing trees ha^{-1} occurring in urban greenspace over 300 years. Scenarios were based on either: (1) a management strategy that manipulates only a single variable up to the maximum value defined in our regression model described above, or (2) a combined management strategy that manipulates all three variables for a set of values that we deemed most practicable for urban landscapes given other socio-economic constraints. Variables not manipulated were fixed at their mean values under existing management practices. In all simulated scenarios, management actions were assumed to take effect immediately. Statistical analyses were completed using GenStat (15th edition, VSN International Ltd, Hemel Hempstead, UK).

Results

We recorded a total of 4,865 trees belonging to 16 eucalypt species. Of those trees, 85% (4,111 trees) were recorded in nature reserves and 15% (754 trees) in urban greenspace. The key difference between tree populations in nature reserves and urban greenspace was the number of seedlings recorded in the 0.1-10 cm DBH cohort (Figure 2). In reserves, we recorded 315 seedlings ha^{-1}, which was 13 times the number recorded in urban greenspace, with 25 seedlings ha^{-1}.

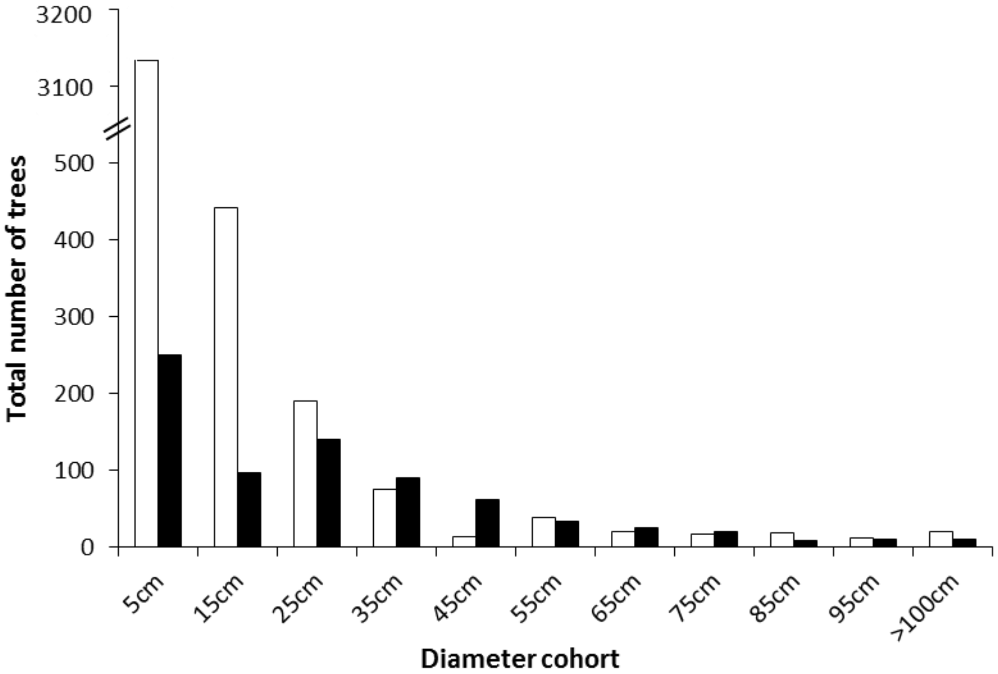

Figure 2. Frequency distribution of median tree diameter cohorts for tree stands (all species) in nature reserves (open bars) and urban greenspace (solid bars).

The availability of hollow-bearing trees under existing management practices

In urban greenspace, we found that under existing management practices, the mean number of hollow-bearing trees ha^{-1} is predicted to decline by 87% over 300 years from an initial recorded stand density of 5.74 trees ha^{-1} to 0.76 trees ha^{-1} (Figure 3). Conversely, in nature reserves, hollow-bearing tree densities fluctuate around a relatively stable mean density of 13.4 trees ha^{-1}. Prediction intervals for urban greenspace were more variable around the mean than for nature reserves. This is driven by highly variable standing lives that trees are permitted to reach in different urban greenspaces (i.e. 60-500 years old). Prediction intervals indicate that under a worst case scenario (i.e. lower 95% prediction interval) all hollow-bearing trees may be lost from urban greenspace within 115 years. Even under a best case scenario (i.e. upper 95% prediction interval) hollow-bearing trees steadily decline over time.

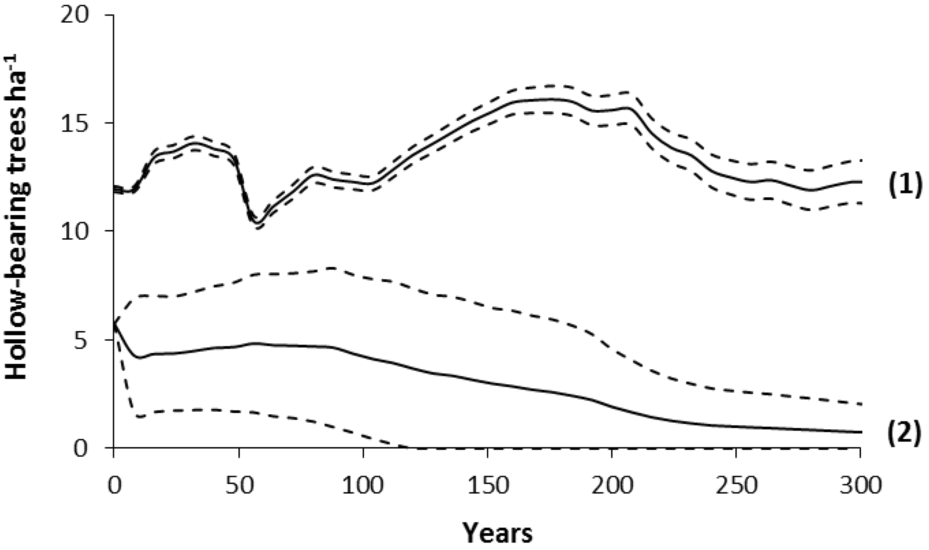

Figure 3. Simulations predicting the relative number of hollow-bearing trees ha^{-1} (mean ± 95% prediction interval) over 300 years under existing management practices in nature reserves (1) and urban greenspace (2).

Variables that can be manipulated to mitigate the decline of hollow-bearing trees

Sensitivity analysis revealed that the mean number of hollow-bearing tree ha^{-1} was most sensitive to: (1) the maximum standing life of trees; (2) the number of seedlings ha^{-1}; and (3) the rate of hollow formation (Table 2). The mean number of hollow-bearing trees ha^{-1} was least sensitive to the period between regeneration events and annual mortality. We also did not identify meaningful interactions between maximum standing life and annual mortality, maximum standing life and the rate of hollow formation, and the number of seedlings ha^{-1} and the period between regeneration events.

1. Maximum standing life

The number of hollow-bearing trees perpetuated in urban greenspace over the long term was most sensitive to the maximum standing life of trees (variance ratio = 138.61). We predicted that hollow-bearing trees would increase in urban greenspace by approximately 0.8 trees ha^{-1} (22%) for each additional 50 years that trees are permitted to remain standing (Figure 4A).

2. Number of seedlings

The number of seedlings ha^{-1} also contributed to the number of hollow-bearing trees perpetuated in urban greenspace over the long term, although relative to maximum standing life this contribution was smaller (variance ratio = 13.81). We predicted that for every 10 additional native seedlings ha^{-1}, the number of hollow-bearing trees would increase by 0.3 trees ha^{-1} (10%; Figure 4B). However, we predicted that to perpetuate hollow-bearing trees even marginally above existing levels will require at least 30 seedlings ha^{-1} and all trees to remain standing for at least 200 years (Figure 5A).

3. Rate of hollow formation

Similarly, the rate of hollow formation also contributed to the number of hollow-bearing trees perpetuated in urban greenspace over the long term, although relative to maximum standing life this contribution was smaller (variance ratio = 11.04). We predicted that hollow-bearing trees would increase by 0.2 trees ha^{-1} (8%) for every 0.5 increase in the rate of hollow formation (Figure 4C). However, we predicted that to perpetuate hollow-bearing trees even marginally above existing levels will require accelerating hollow formation to a rate of 2.5 (i.e. a 44% increase above the observed mean rate) and all trees to remain standing for at least 200 years (Figure 5B).

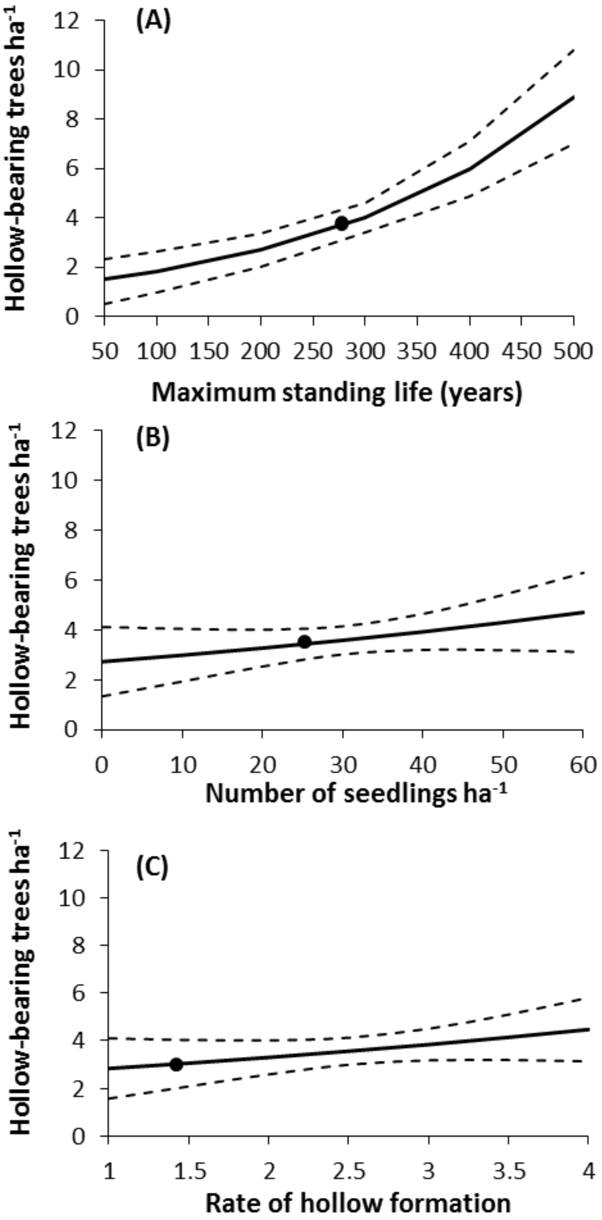

Figure 4. The predicted relative number of hollow-bearing trees ha^{-1} (mean ± 95 prediction intervals) in urban greenspace over 300 years for a range of values for each significant explanatory variable derived from a sensitivity analysis. Significant variables include: the maximum standing life of trees (A); the number of seedlings ha^{-1} (B); and the rate of hollow formation (represented by the coefficient for the probability of hollow occurrence; C). Predicted thresholds under existing management practices are provided for reference (solid circles).

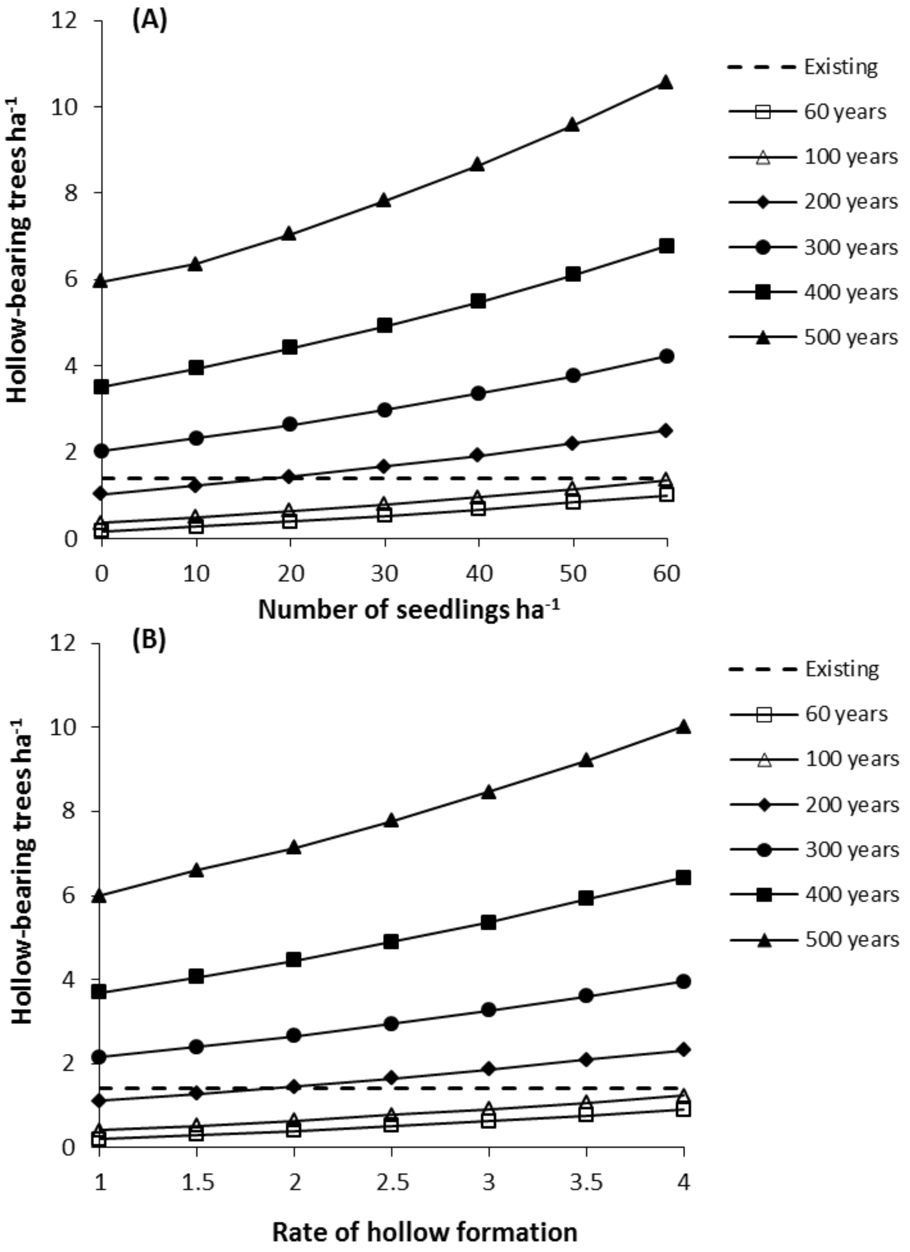

Figure 5. The predicted relative mean number of hollow-bearing trees ha^{-1} in urban greenspace over 300 years for a combination of values for: the maximum standing life of trees and the number of seedlings ha^{-1} (A); and the maximum standing life of trees and the rate of hollow formation (represented by the coefficient for the probability of hollow occurrence; B).

The availability of hollow-bearing trees under alternative management strategies

1. Isolated management approach

If tree standing life were maximised to 500 years and all other variables were unchanged (i.e. held at their mean values under existing management practices), then the mean number of hollow-bearing trees in urban greenspace is predicted to still decline by 64% over the long term, from an initial stand density of 5.74 trees ha^{-1} to 2.09 trees ha^{-1} (Figure 6). If the number of seedlings ha^{-1} were increased only to 60 seedlings ha^{-1}, then the mean number of hollow-bearing trees in urban greenspace is predicted to still decline by 53% over the long term, from an initial stand density of 5.74 trees ha^{-1} to 2.68 trees ha^{-1}. If hollow formation were accelerated only to a rate of 3.7 (i.e. the maximum rate of hollow formation observed for living trees and a 62% increase above the observed mean rate), then the mean number of hollow-bearing trees in urban greenspace is predicted to initially increase to 9 trees ha^{-1} in the short term, but decline by 92% to 0.46 tree ha^{-1} over the long term.

2. Combined management approach

In contrast, a combined management approach that manipulates all sensitive explanatory variables is predicted to increase the number of hollow-bearing trees ha^{-1} over the long term (Figure 6). To achieve this will require at least: (1) increasing the standing life of trees to 450 years (approximately 40% longer average lifespans); (2) increasing the number of seedlings to 60 seedlings ha^{-1} (approximately 60% greater regeneration rate); and accelerating hollow formation up to a rate of 2.0 (approximately 30% greater hollow formation rate; see Table 3). Under this scenario, the density of hollow-bearing trees will initially need to be actively increased in the short term by accelerating hollow formation to achieve at least 7 hollow-bearing trees ha^{-1}. Over time, the density of hollow-bearing trees is predicted to first gradually decline before an increase occurs within 250 years.

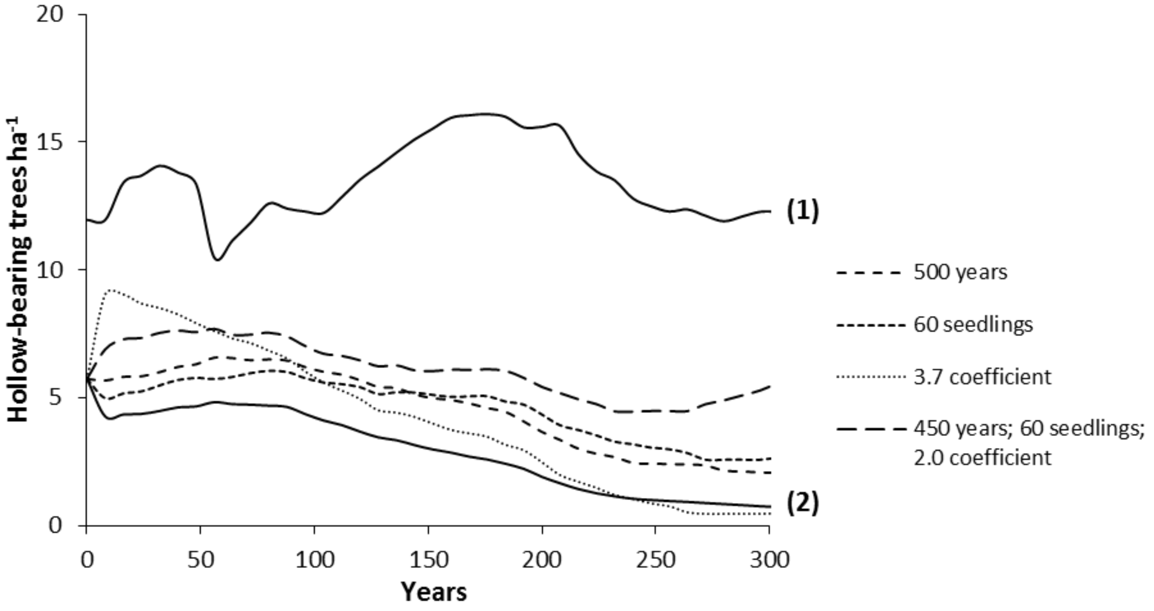

Figure 6. The predicted relative mean number of hollow-bearing trees ha^{-1} over 300 years under a series of alternative urban tree management scenarios (dashed lines). Simulated scenarios include: increasing the standing life of trees only up to 500 years; increasing the number of seedlings only up to 60 ha^{-1}; accelerating hollow formation only by 62% above the observed mean rate (as represented by the coefficient for the probability of hollow occurrence); and a combined management approach (i.e. our recommended management proposal), which manipulates all three variables simultaneously. Scenarios under existing management practices are provided for reference by solid black lines for nature reserves (1) and urban greenspace (2).

Discussion

Large old trees support unique habitat structures (e.g. hollows, coarse woody debris), which form over extensive time periods and cannot be provided by younger trees [e.g. 5, 6]. The decline of large old trees in modified landscapes is a global conservation issue that has serious implications for biodiversity [e.g. 11]. To date, few studies have addressed this problem in urban landscapes, which is a growing concern given the unprecedented rates of urbanisation in cities worldwide [e.g. 25]. Using a simulation model, we investigated the decline of large old trees in an urban landscape over centuries. We predicted that hollow-bearing trees (a surrogate for large old trees) will decline by 87% over 300 years in urban greenspace under existing management practices. Under a worst case scenario, hollow-bearing trees may be entirely lost from urban greenspace within 115 years. Our analysis revealed that the decline of hollow-bearing trees in urban greenspace is most sensitive to: the maximum standing life of trees, the number of regenerating seedlings ha^{-1}, and the rate of hollow formation. To mitigate the decline of large old trees in urban greenspace over the long term, we recommend a management strategy that collectively: (1) maximises the standing life of trees, (2) increases tree regeneration rates, and (3) accelerates the formation of habitat structures provided by large old trees. These results, and the methods used, have important implications for ecologically sustainable urban development.

Existing management practices

Our results provide further evidence that urban landscapes face a concerning future of large old tree decline, which is comparable with other highly impacted landscapes, including agricultural land [e.g. 12, 57] and production forests [e.g. 15, 52]. We argue that predicted declines in hollow-bearing trees in urban greenspace (Figure 3) will not only negatively impact hollow-dependent fauna (e.g. birds, bats, mammals and invertebrates), but also will impact a much wider range of plant and animal species that rely on large old trees and associated habitat structures (e.g. coarse woody debris, litter, peeling bark) for a range of purposes (e.g. foraging, spatial connectivity, epiphyte attachment). Ultimately, these species may face local extinction in urban landscapes. This is supported by recent research, which demonstrates that the removal of large old trees from existing urban habitats will likely impact animal populations [e.g. threatened beetles in Rome, Italy; 20] and community assemblages [e.g. woodland bird communities in Canberra, Australia; 19].

Predictions under existing management practices also highlight the important role that nature reserves play in bridging resource gaps across urban landscapes. In contrast to urban greenspace, we predicted that nature reserves adjacent to urban areas provide a relatively stable supply of hollow-bearing trees over time. Therefore, maintaining and establishing nature reserves in urban environments will likely provide important habitat refuge for species over the long term. However, nature reserves only represent a small proportion of the urban landscape and on their own are unlikely to achieve biodiversity conservation targets [e.g. 58]. In addition, many species rely on networks of multiple habitat trees that extend over large areas of the landscape, including urban habitats [e.g. 59]. For these reasons, we strongly encourage management strategies that focus on arresting large old tree decline within the ‘working’ urban matrix. This means that a re-evaluation of existing management practices in urban landscapes is needed to address the underlying drivers of tree decline.

Alternative management strategies

Large old trees are especially susceptible to removal in urban landscapes worldwide [e.g. Rome, Italy; 20, Bangalore, India; 28, Helsinki, Finland; 29, Canberra, Australia; 60]. With this in mind, we have formulated a set of targeted recommendations, based on results from our analyses, which we anticipate to be relevant to practitioners in a wide range of urban landscapes where trees are maintained.

1. Maximise tree standing life

A major source of tree mortality in urban landscapes is due to managed tree removal [e.g. 20]. This is facilitated by public safety policies and practices, which aim to minimise risk of injury to people and damage to property due to falling trees and branches. For example, in our study area it is estimated that by 2050, approximately 175,600 street trees (24% of all trees in urban greenspace) will have reached their safe standing life (ranging from 60 to 100 years old) and are likely to be removed [54]. Consequently, large old trees, hollow-bearing trees, dead trees and decaying branches are most susceptible to targeted removal prior to reaching their full potential in terms of forming and providing suitable habitat. We found that the number of hollow-bearing trees perpetuated in urban greenspace over the long term was most sensitive to the maximum standing life of trees (Table 2; Figure 4A). Increasing the standing life of all trees by 50 years is predicted to increase the number of hollow-bearing trees ha^{-1} in urban greenspace by 22% over the long term.

Policymakers need to recognize the important habitat resources provided by large old trees and accordingly formulate or amend tree management protocols so that large old trees are afforded better protection. This may involve re-evaluating criteria used to guide tree felling decisions [e.g. 29]. Practical strategies that maximise the safe standing life of trees should also be implemented. This may involve: (1) allowing trees to age more naturally in urban greenspace frequented less by members of the public and where risk to people and property is minimal (e.g. derelict land, areas along stormwater wetlands, and some parklands); (2) avoiding structural damage to trees (e.g. damage to roots due to road works); (3) creating safe zones or barriers that separate the public from potentially hazardous trees thereby minimising safety risks (e.g. landscaping around the base of the tree using shrubs); (4) physically re-enforcing the structural integrity of large, old trees (e.g. supporting frames, cables or poles); and (5) safely retaining dead trees wherever possible. However, our results indicated that management strategies that only maximise the standing life of trees will be insufficient at mitigating the decline of hollow-bearing trees over the long term (Figure 6).

2. Increase tree regeneration

We found that the rate of tree regeneration in urban greenspace (both natural and planted) was 13 times lower than in nature reserves (Figure 2). A lack of young trees is a major contributing factor of large old tree decline in urban greenspace over the long term. Older trees that eventually die and are removed from any given landscape need to be replaced by younger trees, thereby perpetuating the formation of important habitat structures over multiple generations [e.g. 18, 61]. We predicted that increasing tree regeneration by 10 native seedlings ha^{-1} would increase the number of hollow-bearing trees in urban greenspace by 10% over the long term (Figure 4B).

Tree regeneration in urban habitats is typically achieved through planting initiatives and encouraging natural regeneration. Increasing the number of planted trees through government and community initiatives should increase the number of young trees persisting in urban habitats [e.g. 62]. However, in some urban greenspace (e.g. roadside margins and residential areas), tree planting can be logistically challenging as practitioners need to balance multiple socio-economic and ecological factors when implementing planting strategies, including: site location, public safety, aesthetics, land ownership, and existing vegetation [e.g. 63]. Furthermore, reducing seedling mortality in urban habitats is also an important consideration that may require additional protection measures and costs [e.g. tree guards, supporting posts; 64]. In some urban greenspace (e.g. parklands, wetlands) it may be more cost-effective over the long term to promote natural regeneration. Natural regeneration in urban habitats is predominantly limited because of: unfavourable seedbed conditions (e.g. impervious surfaces, pollution, and nutrient runoff), increased competition from invasive plants, and increased mortality due to mowing and pedestrian traffic [e.g. 31, 65]. Strategies that promote natural regeneration could involve: fencing-off areas with existing re-growth, increasing public awareness of regenerating areas through signage, and enhancing local microclimates that favour seedling establishment and survival [e.g. retaining litter and logs; 31, 66]. However, our results indicated that management strategies based solely on increasing tree regeneration will be insufficient at mitigating the decline of hollow-bearing trees over the long term (Figure 6).

3. Accelerate the formation of habitat structures provided by large old trees

The formation of habitat structures such as hollows is a slow process more likely to occur in large old trees [35]. This is because trees with compromised structural integrity are more susceptible to wood decay resulting in the formation of hollows and other structures such as fallen logs and dead branches. Strategies promoting the formation of habitat structures by artificial means can bypass the time needed for these structures to form naturally. Our results indicate that the density of hollow-bearing trees could be increased in urban greenspace by accelerating hollow formation (Figure 4C).

Accelerating hollow formation in urban areas is commonly achieved by replicating hollow structures, such as installing artificial nest boxes [e.g. 32]. However, in urban areas, there are limitations with artificial habitat structures, including: occupancy by pest species, poor rates of target species occupancy, and rapid rates of attrition through collapse and decay of materials [e.g. 67]. It may also not be feasible or practicable to install and maintain artificial habitat structures in large enough numbers across extensive areas over centuries. Therefore, strategies that accelerate the formation of habitat structures by other means should also be explored [e.g. 68]. Methods previously proposed for hollows include: tree ringbarking or girdling [e.g. 69], canopy topping [e.g. 70], controlled fire burns [e.g. 71], and injecting trees with herbicides [e.g. 72]. These strategies are also likely to accelerate the formation of other important habitat structures provided by large old trees, including dead branches and coarse woody debris. In urban landscapes, sub-lethal methods of accelerating habitat structure formation are most preferable to also avoid compromising public safety. This may involve only partially injuring trees [e.g. carving out hollows on trunks and some branches; 73] and using more invasive methods on trees with large diameters that are structurally robust in order to also maximise tree standing life [35]. More research is still needed to investigate methods aimed at accelerating habitat structure formation, especially in urban landscapes. Nevertheless, our results highlight that management strategies based solely on accelerating hollow formation can be effective at increasing the density of hollow-bearing trees in the short-term, but not over the long term (Figure 6).

4. Our management proposal

Our results emphasise that a combination of different management approaches, aimed at improving multiple aspects of tree management and maintenance, are needed to perpetuate hollow-bearing trees in urban greenspace over the long term (Figure 5). We propose a management strategy based on simultaneously manipulating all three explanatory variables discussed above, which were identified as being the most sensitive model parameters in our analyses. Under this scenario (Figure 6), we predicted that the decline of hollow-bearing trees in urban greenspace can be arrested within 250 years if: (1) trees remain standing for at least 450 years ensuring that they reach their maximum habitat potential; (2) at least 60 seedlings ha^{-1} are planted or naturally regenerated; and (3) hollow formation is accelerated to a rate of 2.0 in the short term by installing nest boxes and sub-lethally creating hollows by other methods (see Table 3). Our proposal considers the complexities associated with managing urban greenspaces for multiple purposes, including recreation and conservation. We recognize that it may not be possible to retain all trees to their maximum biological age due to public safety risks. It may also not be practical or feasible to accelerate the formation of habitat structures artificially on a large enough scale over prolonged time periods. Instead, we attempt to balance socio-economic and biodiversity benefits by combining multiple tree management and maintenance approaches in an achievable manner. Future research should also aim to investigate alternative management scenarios from a more financial perspective, which too would benefit practitioners (e.g. numbers of hollow-bearing trees gained per management dollar spent). However, even under our proposed management strategy, the density of hollow-bearing trees is predicted to first decline, or undergo a bottleneck, before increasing. This is because of an extinction debt or the time lag between implementing management actions and actually observing an increase in hollow-bearing trees. Delaying mitigation is anticipated to further exacerbate the effects of time lags and require more drastic measures at greater costs to reverse tree declines [e.g. 26]. Immediate action will likely also reduce bottlenecks in urban plant and animal populations that depend on large old trees for survival.

Conclusion

We have quantified the decline of hollow-bearing trees in an urban landscape over centuries. We provided a novel assessment of the conservation implications associated with existing tree management practices and the efficacy of a range of alternative management strategies. It is evident from our results that existing urban tree management practices require urgent re-evaluation if hollow and tree-dependent biodiversity are to be maintained in urban landscapes. We recommend that: (1) large old trees are afforded better protection and remain standing over longer time periods; (2) tree regeneration is actively improved so that large old trees lost over time are replaced by younger trees; and (3) the formation of habitat structures provided by large old trees is accelerated to compensate for short term deficits in resource availability. Immediate implementation of these recommendations is needed to arrest the decline of large old trees, avoid lag effects, and avert long term risk to biodiversity in urban landscapes.

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Supporting information

Table S1. List of recorded tree species and diameter size class distributions.

A. Nature reserves	**Tree species**	**Diameter size class (cm)**										
		0.1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	>100
	E. blakelyi (Blakely's red gum)	1,595	122	39	27	3	16	9	4	5	8	9
	E. bridgesiana (apple box)	244	58	49	9	1	6	2	2	3	0	2
	E. dalrympleana (mountain gum)	1	0	0	0	0	0	0	1	0	0	0
	E. dives (broad-leaved peppermint)	10	0	0	1	1	0	1	0	0	0	0
	E. goniocalyx (bundy)	0	0	1	0	0	0	0	0	0	0	0
	E. macrorhyncha (red stringybark)	60	39	17	7	2	0	2	0	0	0	1
	E. mannifera (brittle gum)	5	0	0	1	1	0	1	0	0	0	0
	E. melliodora (yellow box)	948	153	57	20	5	13	3	8	9	2	12
	E. nortonii (mealy bundy)	2	0	0	0	0	0	0	0	0	0	0
	E. polyanthemos (red box)	69	34	9	2	0	0	1	2	0	0	0
	E. rossii (scribbly gum)	216	32	21	10	1	4	2	0	0	1	1
	Dead trees	38	43	9	7	3	4	3	2	1	1	0
Sum		**3,188**	**481**	**202**	**84**	**17**	**43**	**24**	**19**	**18**	**12**	**25**
B. Urban greenspace												
	E. blakelyi (Blakely's red gum)	90	22	29	23	11	5	4	6	2	3	5
	E. bridgesiana (apple box)	14	4	12	3	0	1	0	0	0	0	0
	E. dalrympleana (mountain gum)	1	0	0	1	2	0	2	1	3	0	0
	E. delegatensis (alpine ash)	0	0	0	0	1	0	0	0	0	0	0
	E. dives (broad-leaved peppermint)	1	1	2	5	4	3	1	1	2	0	0
	E. fastigata (brown barrel)	0	0	3	0	2	0	0	0	0	0	0
	E. goniocalyx (bundy)	1	2	0	2	0	0	0	0	0	0	0
	E. macrorhyncha (red stringybark)	0	1	0	2	4	3	3	1	0	1	1
	E. mannifera (brittle gum)	20	21	37	26	11	7	3	2	1	0	0

	E. melliodora (yellow box)	68	26	29	10	11	10	3	4	1	4	6
	E. nortonii (mealy bundy)	2	1	1	1	1	0	0	0	0	0	0
	E. polyanthemos (red box)	1	8	5	3	1	0	1	0	0	0	0
	E. rossii (scribbly gum)	38	6	4	1	0	0	0	1	0	0	0
	E. rubida (candlebark)	8	1	2	4	4	0	0	1	0	0	0
	E. sideroxylon (ironbark)	1	5	7	2	2	3	4	1	0	0	0
	E. viminalis (ribbon gum)	4	3	8	9	5	3	2	2	0	1	1
	Dead trees	1	1	0	3	0	0	0	0	0	0	0
Sum		**249**	**102**	**139**	**95**	**62**	**35**	**23**	**20**	**9**	**9**	**13**

Summary S1: A description of simulation model functionality as applied to our analyses

The simulation model we used in our paper to predict the size-class distribution of trees in stands over time was developed using Visual Basic in Microsoft Excel and can be obtained from the authors on request. This simulation model is also described with respect to the management of scattered trees in agricultural landscapes [1], mature trees in wood production forests [2], and nest trees for a threatened species in [3].

This simulation model tracks the mean diameter at breast height (DBH) of trees in cohorts through time. For this exercise, we separately simulated trees in reserves and urban areas. We employed a Monte Carlo approach to simulation, whereby parameters in the model can be entered as random values within a range of observed or likely values so the predictions reflect the uncertainty of these parameters. The model is then run as many times as is specified (in this instance all predictions were based on 300 runs of the model), so predictions for any single scenario are a summary of values from multiple runs of the model. There are six key steps in the simulation.

Step 1 – Record the numbers of trees by size-class

The simulation commences with data on the mean number of trees in 10 cm diameter classes (i.e., 0-10 cm, 11-20 cm, etc.) for each tree species group (species distributions summarised in Table S1). Initial values at the commencement of the simulation (T=0 years) were based on data collected at 200 50 m x 20 m (0.1 ha) plots in urban and nature reserve sites within our study area. These data are expressed as a per ha basis for each simulation.

Step 2 – Estimate the numbers of trees with hollows

We predicted the proportion of trees that contained hollows separately for each tree species group and DBH cohort based on visual estimation of the presence/absence of hollows in trees across the study area using the equation

$$\mathit{Logit\ (Pr.\ Hollows)} = -7.112 + (0.086 \times \text{DBH}) + (\text{species group estimate}) \qquad \text{[Equation 1]}$$

The area under the receiver operating characteristic curve of this statistical model was 0.92, indicating that its discriminating ability was excellent [4].

Step 3 – Grow trees for *t* years

To simulate tree-growth over time, we developed a relationship between tree age and DBH using the following equation developed by [5]:

$$\text{Age} = 0.02 \times \pi \times (\text{DBH}_{\text{standardized}} /2)^2 \qquad \text{[Equation 2]}$$

where $\mathrm{DBH}_{\mathrm{standardised}}$ is the yellow box (*Eucalyptus melliodora*) equivalent diameter for each tree as defined below. Data on the relationship between age and DBH only exist for one tree species (yellow box) in our study area [6]. To predict the ages of trees of other species, we followed the procedure outlined by [5] and calculated a yellow box equivalent diameter for each individual tree of the other eucalypt species. The procedure assumed that all eucalypt species in our study area follow an identical growth curve relative to their maximum attainable diameter, and have the same approximate life-span as yellow box. DBH values for all tree species were initially standardised as a proportion of the maximum attainable diameter for that species observed in the field. Those values were then multiplied by the maximum diameter observed for yellow box (151 cm) to obtain a yellow box equivalent diameter. We acknowledge that this procedure is unlikely to give precise age estimates, but it is a pragmatic solution given the paucity of data on tree ages available for trees in our study area. However, previous research [1,2] indicates that the number of mature trees perpetuated over time is not sensitive to this variable. The initial age of trees in each cohort is predicted by using the median DBH of each cohort in Equation 2, *t* years is added to this age (where *t* is the years between recruitment events) and then the inverse of Equation 2 is used, in turn, to predict the new DBH of the cohort after *t* years.

Step 4 – Recruit a specified number of trees at the beginning of each time-step

We recruited *n* new trees per ha into each landscape type (urban and reserve) every *t* years. For the *status quo* scenarios, *n* was the mean number of trees by tree species group in the smallest DBH class within each landscape and *t* was the age of this cohort (estimated using Equation 2). Recognising that tree recruitment can be highly variable from year to year, the value for *n* for each tree species group in each landscape type for the *status quo* scenarios was a random value drawn from a Poisson distribution with a mean taken from the smallest diameter cohort (0-10 cm DBH) for trees in each species group within each landscape type. For the alternative management scenarios in urban areas, we chose random values from a uniform distribution. Runs with negative values for recruitment were treated as zero recruitment.

Step 5 – apply tree mortality

We applied two sources of mortality during each time-step. We calculated tree mortality from data collected on changes in the mean numbers of trees in each DBH cohort, reflecting the density-dependent nature of tree mortality in natural stands. This was given as

$$1 - s^{(1/y)} \qquad \text{[Equation 3]}$$

where *s* is the proportion of trees that survive from one cohort to the next, and *y* is the number of years between recruitment events.

For trees in reserves, we set 500 as the maximum number of years that trees will remain living, which is based on longevity estimates for yellow box reported by [6]. There were no other data from which this estimate could be derived and [1] reports that the number of scattered trees is not sensitive to this parameter in simulations of this type. For urban areas, the maximum number of years that trees remain living was selected randomly from a uniform distribution between 60-500 years, reflecting the existing policy of the government in our study area to remove trees as young as 60 years old for safety reasons. Once a tree had died, we allowed it to remain standing for 50 years in reserves, but in urban areas we removed the tree immediately in keeping with management practices in our study area.

At the completion of this step the number of surviving trees by DBH class and species group was tallied.

The predicted proportion of hollow-bearing tree was then multiplied by the mean numbers of surviving trees in each DBH cohort to arrive at a predicted number of trees with hollows at the end of each time-step (*t*).

Steps 1-5 are repeated such that *t* (the period between regeneration events) is added to *T* (the total length of the simulation) until *T*=300 years. We reported the mean (±95% prediction interval) for all runs of the simulation model at each time-step between 0 and 300 years.

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Paper III. The value of scattered trees for biodiversity: contrasting effects of landscape context and tree size

In Paper II, I found that large old trees are predicted to decline in urban landscapes. I also discussed some of the key challenges associated with managing mature trees in human-dominated environments. In Paper III, I conducted a multi-taxonomic experiment to determine if scattered trees in modified landscapes are used by wildlife. I quantified invertebrate, bat and bird responses at individual trees of different sizes located in different landscape contexts.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2015). The value of scattered trees for biodiversity: contrasting effects of landscape context and tree size. Under review: *Diversity and Distributions*.

Abstract

Aim: The biodiversity value of scattered trees in modified landscapes is often overlooked in strategic land planning and conservation priorities. We conducted a multi-taxonomic experiment 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, southeastern Australia

Methods: Invertebrate, bat and bird surveys were undertaken over three years (2012-14) 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. Invertebrate abundance and richness did not differ significantly at trees across landscape contexts, highlighting that resources in modified landscapes can sustain invertebrate populations. However, invertebrate 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 for all bat species 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 invertebrates 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. Synergistic land management strategies are needed to collectively account for responses exhibited by multiple taxa at varying spatial scales. Priorities should include: (1) planning for mosaics of land-use types; and (2) retaining and perpetuating scattered trees. In practice, these strategies could provide crucial habitat benefits to a multitude of species in human-modified landscapes.

Keywords: bats, birds, conservation planning, human-modified landscapes, large old trees, invertebrates

Introduction

Landscape modification is the biggest global threat to terrestrial biodiversity (Grimm *et al.*, 2008; Phalan *et al.*, 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 (Vitousek *et al.*, 1997; Millenium Ecosystem Assessment, 2005). Human-altered landscapes not specifically devoted to nature conservation can still provide important habitat opportunities for species but also present unique challenges for biodiversity conservation (McKinney, 2006; Lindenmayer *et al.*, 2008; Driscoll *et al.*, 2013). 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 *et al.*, 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 now widely recognized that when applied to non-insular, human-modified landscapes, species responses often defy biogeographic predictions (i.e. habitat-isolation and species-area relationships; Fischer & Lindenmayer, 2002a; Mendenhall *et al.*, 2014). Many species do not perceive fragmented landscapes as simple binary units of 'habitat' versus 'non-habitat' (Franklin & Lindenmayer, 2009; Didham *et al.*, 2012). Alternative conceptual frameworks, like the 'habitat variegation model' (McIntyre & Barrett, 1992) and 'continuum model' (Fischer & Lindenmayer, 2006) offer more holistic wildlife-oriented approaches recognising 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 isolated and small habitat resources (e.g. individual trees) through to intact and large habitat patches (e.g. nature reserves). Nevertheless, many applied management policies and practices remain skewed towards a traditionalist conservation framework governed by biogeographic principles, which advocate that 'intact' and 'large' is 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 conserving isolated habitat resources dispersed within disturbed landscapes, which may also yield considerable benefits for biodiversity (Moilanen *et al.*, 2009; Cunningham *et al.*, 2014).

Scattered trees (*sensu* Manning *et al.*, 2006) are prominent features of human-modified landscapes worldwide and have been identified as ‘keystone ecological structures’. That is, scattered trees can provide disproportionate habitat for biota relative to their size and availability (Lindenmayer *et al.*, 2013). For example, scattered trees in commercial production forests (Mazurek & Zielinski, 2004; Matveinen-Huju *et al.*, 2006), agricultural landscapes (Dunn, 2000; DeMars *et al.*, 2010), and urban environments (Yasuda & Koike, 2009; Stagoll *et al.*, 2012) have all been shown to significantly contribute to wildlife diversity. Locally, scattered trees provide distinct microclimates and unique structural elements like hollows and woody debris (Tews *et al.*, 2004; Manning *et al.*, 2012). At a landscape scale, scattered trees increase spatial heterogeneity and connectivity that can aid species dispersal (Fischer & Lindenmayer, 2002b; Manning *et al.*, 2009).

Despite growing empirical evidence demonstrating their ecological importance, scattered trees are in decline in ecosystems around the world (Lindenmayer *et al.*, 2012). Tree retention in modified landscapes can be a highly contentious issue that conflicts with human interests and activities including: logging (Laurance *et al.*, 2000), wood production (Lutz *et al.*, 2009), crop cultivation (Gibbons *et al.*, 2008), livestock grazing (Fischer *et al.*, 2010b), urbanisation (Le Roux *et al.*, 2014a) and the public safety of residents (Carpaneto *et al.*, 2010). Scattered trees thus often lack formal protection and are regularly overlooked in strategic land planning and conservation priorities (Stagoll *et al.*, 2012; Hartel *et al.*, 2013; Plieninger *et al.*, 2015). The underlying assumption that scattered trees have limited biodiversity value because they are isolated and located in highly degraded or human-dominated landscapes underpins many policies and practices that facilitate intentional tree removal (Manning *et al.*, 2006; Gibbons *et al.*, 2009; Le Roux *et al.*, 2014b). Effectively, scattered trees may be ‘triaged’ or sacrificed in favour of the preservation of larger, intact habitat patches (e.g. exemptions to paddock tree removal in land clearing legislation in parts of Australia; NSW Government, 2014). But is this land management and conservation approach justified?

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 multi-taxonomic experiment at individual trees targeting invertebrates, bats and birds. We tested two null hypotheses based on the premise that many real-world conservation and management practices remain largely governed by an overextension of biogeographic principles. That is, conservation efforts are prioritised for more intact and larger habitat patches (reserves), while isolated and smaller habitat resources (scattered trees) remain largely overlooked or ‘triaged’.

> *Hypothesis 1 (landscape context)*: trees located in a more intact semi-natural landscape (reserves) support greater wildlife abundance, richness and more distinct communities compared with more isolated scattered trees located in modified landscapes (pasture, urban parklands, urban built-up areas).

> *Hypothesis 2 (tree size)*: large trees (> 80 cm DBH) support greater wildlife abundance, richness and distinct communities compared with medium (51-80 cm DBH) and small trees (20-50 cm DBH).

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.

Methods

Study area

We conducted our study in Canberra, Australian Capital Territory (ACT), southeastern Australia (35°17′35.64″ S; 149°07′27.36″ E). Canberra covers an area of 810 km^2 and supports a population of 375,000 people (ACT Government, 2011). Native temperate woodlands once dominated the region and are characterised by two species, yellow box (*Eucalyptus melliodora*) and Blakely's red gum (*E. blakelyi*). Tree clearance for farming and urban development has led to an approximately 95% decline in woodland habitat, which is listed as a critically endangered ecological community (Department of the Environment, 2015).

Experimental design

We stratified our study area into four dominant landscape contexts, including: (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)). 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; Fig. 1). This resulted in 12 treatment combinations and 72 sample trees (Tables S1 and S2). Sample trees were spaced > 250 m apart to minimise spatial dependency and were located across nine reserves, four rural landholdings, 18 urban parklands and 18 urban built-up areas, which collectively spanned approximately 50 km^2. 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, $p < 0.05$, Kruskal-Wallis ANOVAs).

Wildlife surveys

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

1. Invertebrates

In each year, we used three sampling techniques to capture invertebrates. First, we used ultraviolet (UV) light traps (Australian Entomological Supplies, Australia) between sunset and sunrise during one night. We secured one UV trap to the trunk of each tree at a height of 1.5 m. Second, we used one glue trap (20 x 10 cm; STV International Ltd, UK) secured to the trunk of each tree at a height of 1.5 m for one night. Third, we conducted a five minute active search at each tree, which involved peeling away bark and inspecting the trunk within a standardized area (30 cm wide x 2 m aboveground). Each sampling method was undertaken on a different day at each tree. We counted and sorted invertebrates into orders (following Zborowski & Storey, 2010).

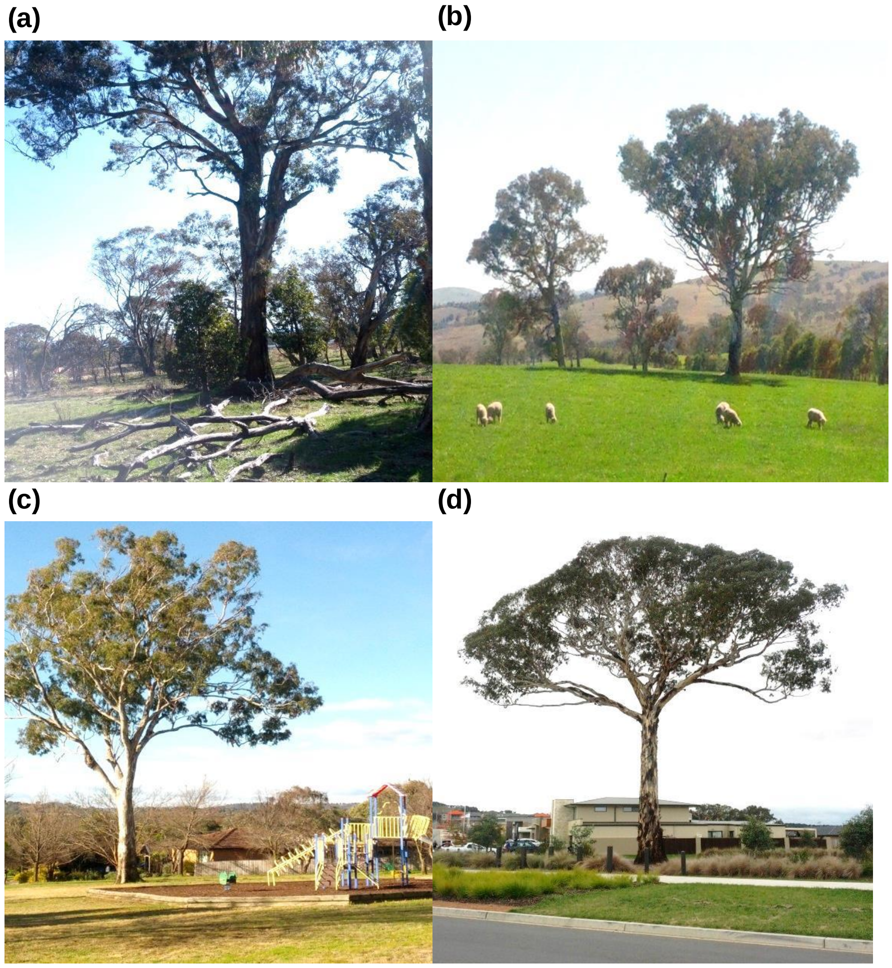


Figure 1. Examples of large (> 80 cm DBH) scattered trees located in different landscape contexts, including; (a) semi-natural reserves; (b) grazed pasture; (c) urban parklands; and (d) urban built-up areas.

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 *et al.*, 2012b). We positioned the detector microphone upwards to restrict recording to the tree (approximately 60 degrees from the horizon). Microphones were directional (detection distance and angle of at least 20 m and 60 degrees, respectively). We processed echolocation passes using AnalookW and Anascheme software (M. Gibson, Ballarat University, unpublished) and a regional call identification key (Adams *et al.*, 2010). Calls from two sympatric long-eared bat species were indistinguishable and classified as a species complex. It was not possible to obtain abundance data from acoustic recordings and we instead used relative bat activity (passes / tree / night). Bat and invertebrate surveys were not undertaken on the same night at each tree.

3. Birds

In each year, we conducted two separate visual fixed point bird surveys at each tree. Each survey was 20 minutes in duration (Fischer & Lindenmayer, 2002c). Surveys involved sitting > 5 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 *et al.*, 1991).

Statistical analyses

1. Abundance and richness

We used generalised linear mixed models (GLMMs) to examine variation in invertebrate, bat (activity) and bird abundance and richness data and to identify the relative effect of explanatory variables. We fitted ‘landscape context’ and ‘tree size’ as fixed effects in a two-way crossed design. We fitted ‘year’ and ‘tree identity’ as random effects to account for repeat surveys across years and at sample trees. We also tested the effects of two covariates: ‘tree species’ (all models); and ‘invertebrate abundance per tree’ (bat and bird models). We fitted normal distributions (identity link) to log-transformed abundance data and Poisson distributions (log link) to richness data. Mantel tests confirmed no spatial autocorrelation occurred between sample trees for wildlife responses (r = -0.002-0.05; p-value < 0.05). Data are presented as means (± SE).

2. Community composition

We used generalised permutational multivariate analyses of variance (PERMANOVAs) to examine variation in invertebrate, bat and bird community composition (Anderson & Robinson, 2003). We further examined PERMANOVA results by performing constrained canonical analyses of principal coordinates using discriminant analysis (CAP (CDA)), which finds axes maximising separation among groups (Anderson & Willis, 2003). Constrained ordination is useful to examine compositional data against hypotheses. In our case, as defined *a priori* by landscape context (Hypothesis 1) and tree size (Hypothesis 2). Correlations between taxa and canonical axes were used to identify taxa that contributed strongly to community distinctiveness (correlations > (±) 0.25). For multivariate analyses, we used a Bray-Curtis dissimilarity index on square root transformed abundance data (bat activity) pooled across survey years with 10,000 permutations.

Results

We recorded a total of: 47,096 invertebrates identified to 19 orders; 30,536 bat echolocation passes assigned to 11 species; and 1,785 birds identified to 61 species (see Table S3 for recorded taxa and scientific names).

Hypothesis 1: Effect of landscape context

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

1. Invertebrates

We found that landscape context had no significant effect on invertebrate abundance and richness (Table 1; Fig. 2a and 2b). However, landscape context did have a significant effect (p = 0.032) on invertebrate community composition (Fig. 3a; see Tables S4 and S5 for statistical summaries). There was a significant pair-wise difference (p = 0.008) between invertebrate communities recorded at trees in urban built-up areas and reserves. In urban built-up areas, we recorded the highest abundance of Coleoptera (beetles), Neuroptera (lacewings) and Hymenoptera (ants, bees and wasps) orders. In reserves, we recorded the highest abundance of Diptera (flies), Lepidoptera (moths and butterflies) and Mecoptera (scorpion flies) orders.

2. Bats

We found that landscape context had a significant effect ($p < 0.001$) on bat activity and richness (Table 1). At trees in urban built-up areas, bat activity and richness were reduced (62.43 ± 10.00 passes / tree; 3.91 ± 0.23 species / tree) compared with urban parklands (164.41 ± 24.16; 5.82 ± 0.22), pasture (220.91 ± 30.34; 7.03 ± 0.25) and reserves (152.93 ± 21.40; 6.52 ± 0.26; Fig. 2c and 2d). Landscape context also had a significant effect ($p < 0.001$) on bat community composition (Fig. 3b). There were significant pair-wise differences ($p < 0.001$) between bat communities recorded at trees in urban built-up areas and all other landscape contexts. We consistently recorded the lowest levels of bat activity in urban built-up areas for all species. Even for species considered tolerant of urban environments, like Gould’s wattled bat (Threlfall *et al.*, 2012b), activity was reduced at trees in urban built-up areas (42.80 ± 9.25 passes / tree) compared with trees in urban parklands (91.40 ± 15.74), pasture (117.00 ± 19.71) and reserves (78.24 ± 17.53). For urban sensitive species, like long-eared bats (Threlfall *et al.*, 2012b), activity was especially low at trees in urban built-up areas (0.13 ± 0.08) compared with trees in urban parklands (0.85 ± 0.34), pasture (3.56 ± 0.66) and reserves (2.35 ± 0.61). Two bat species were recorded only in reserves (eastern false pipistrelle and yellow-bellied sheath-tailed bat).

3. Birds

We found that landscape context had a significant effect on bird abundance ($p < 0.001$) and richness ($p = 0.024$; Table 1). More individuals and species were recorded at trees in pasture (11.33 ± 2.27 individuals / tree; 3.35 ± 0.42 species / tree), urban parklands (9.27 ± 1.83; 3.02 ± 0.36) and urban built-up areas (8.77 ± 0.99; 3.05 ± 0.26) compared with trees in reserves (3.96 ± 0.66; 1.90 ± 0.28; Fig. 2e and 2f). Landscape context also had a significant effect ($p < 0.001$) on bird community composition (Fig. 3c). There were significant pair-wise differences ($p < 0.001$) between bird communities recorded at non-urban trees (reserves and pasture) and urban trees (parklands and built-up areas). Urban trees supported higher abundance of urban-adapted native species (e.g. Australian magpie) while non-urban trees supported higher abundance of hollow-nesting species (e.g. crimson rosella). Some species were recorded only in reserves (e.g. brown thornbill).

Table 1. Summary of main effects for generalized linear mixed models (GLMMs; abundance (or activity) and richness data) and permutational multivariate analyses of variance (PERMANOVAs; assemblage data) for invertebrates, bats and birds.

Response	**Fixed effects**				
	Landscape context	Tree size	Landscape context*tree size	Tree species	Invertebrate abundance / tree
Invertebrate:					
Abundance	0.835	0.360	0.112	0.355	-
Richness	0.167	0.539	0.693	0.212	-
Assemblage	0.032	0.644	0.382	-	-
Bat:					
Activity	< 0.001	0.845	0.427	0.912	0.002
Richness	< 0.001	0.523	0.155	0.989	0.006
Assemblage	< 0.001	0.782	0.972	-	-
Bird:					
Abundance	<0.001	<0.001	0.040	0.005	0.196
Richness	0.024	<0.001	0.235	0.023	0.293
Assemblage	< 0.001	<0.001	0.384	-	-

Hypothesis 2: Effect of tree size

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

1. Invertebrates

We found no significant effect of tree size on invertebrate abundance, richness or community composition (Table 1). We also found no significant effect of tree species on invertebrate abundance and richness.

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, invertebrate abundance at trees had a significant positive effect on bat activity ($p = 0.002$) and richness ($p = 0.006$).

3. Birds

We found that tree size had a significant effect on bird abundance ($p < 0.001$) and richness ($p < 0.001$; Table 1). More individuals and species were recorded at large trees (> 80 cm DBH; 15.65 ± 1.96 individuals / tree; 4.79 ± 0.33 species / tree) compared with medium trees (51-80 cm DBH; 6.25 ± 0.74; 2.43 ± 0.21) and small trees (20-50 cm DBH; 3.11 ± 0.52; 1.28 ± 0.15). We also found a significant ($p = 0.040$) 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 (Fig. 2e and 2f). We found no significant effect of invertebrate abundance on bird abundance and richness. However, tree species had a significant effect on bird abundance ($p = 0.005$) and richness ($p = 0.023$). More individuals and species were recorded at Blakely's red gum (8.88 ± 1.38 individuals / tree; 3.08 ± 0.29 species / tree) and at 'other eucalypt' species (9.01 ± 1.48; 2.76 ± 0.28) compared to yellow box (7.12 ± 1.30; 2.65 ± 0.31).

We found that tree size also had a significant effect ($p < 0.001$) on bird community composition (Fig. 3d). There were significant pair-wise differences between bird communities recorded at large trees and medium trees ($p = 0.026$) and large trees and small trees ($p < 0.001$). Consistently more individuals were recorded at large trees for most bird species, which represented a diversity of functional guilds, including: hollow-nesters (e.g. galah), nectivores (e.g. yellow-faced honeyeater), aerial insectivores (e.g. willie wagtail), habitat generalists (e.g. magpie lark), and urban-adapted native species (e.g. red wattlebird) and exotic species (e.g. common myna). Approximately a quarter (26.2%) of bird species (16 unique species) were recorded only at large trees compared to 11.5% (7 unique species) at medium trees and 3.3% (2 unique species) at small trees. Some guilds also were exclusively recorded at large trees, including raptors (e.g. brown falcon) and threatened species (e.g. superb parrot; Table S3).

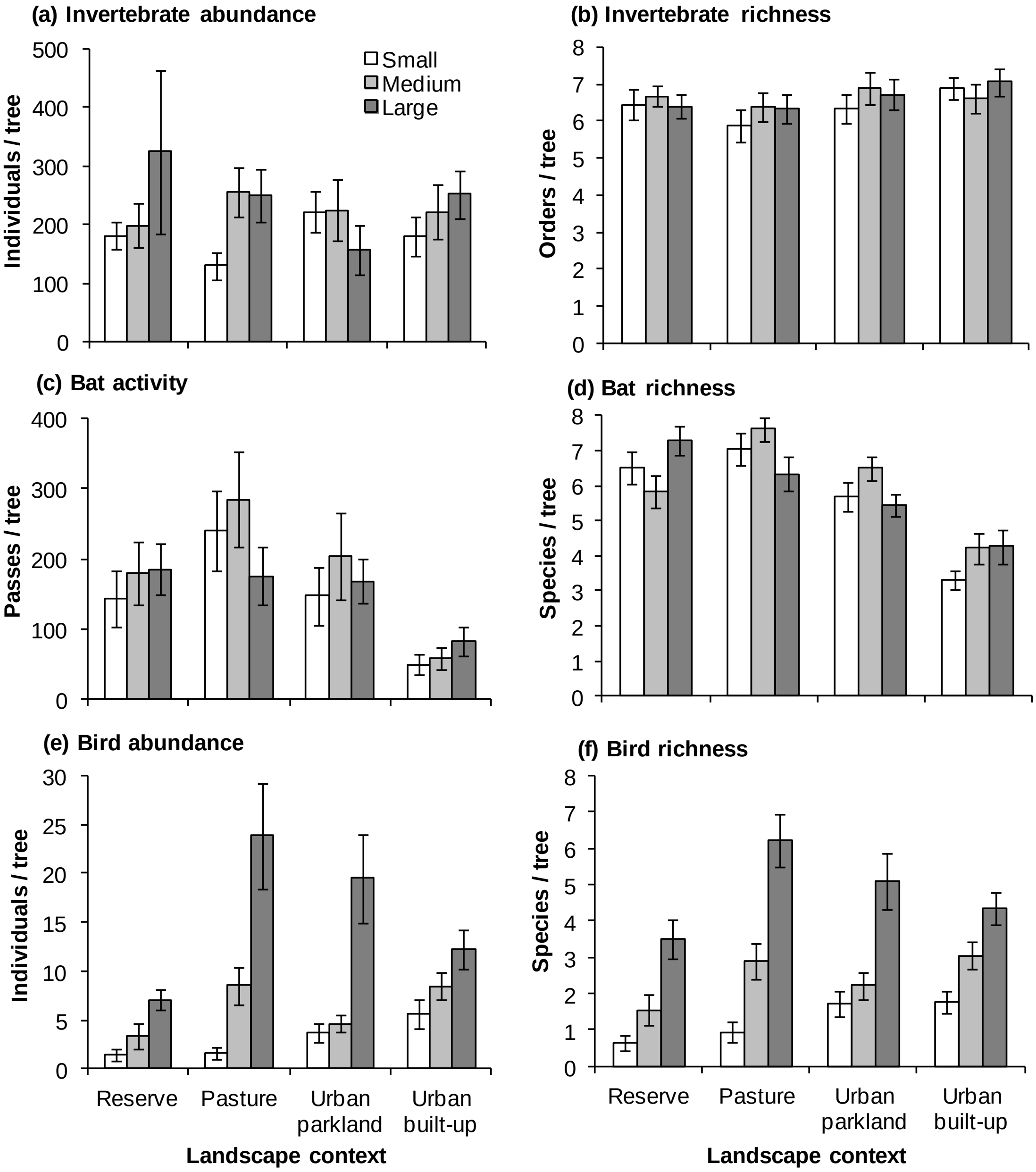


Figure 2. Patterns of variation (means ± SEM) in wildlife abundance and richness across different landscape contexts and tree sizes. Measures of wildlife responses include: (a) invertebrate abundance; (b) invertebrate order richness; (c) relative bat activity; (d) bat species richness; (e) bird abundance; and (f) bird species richness.

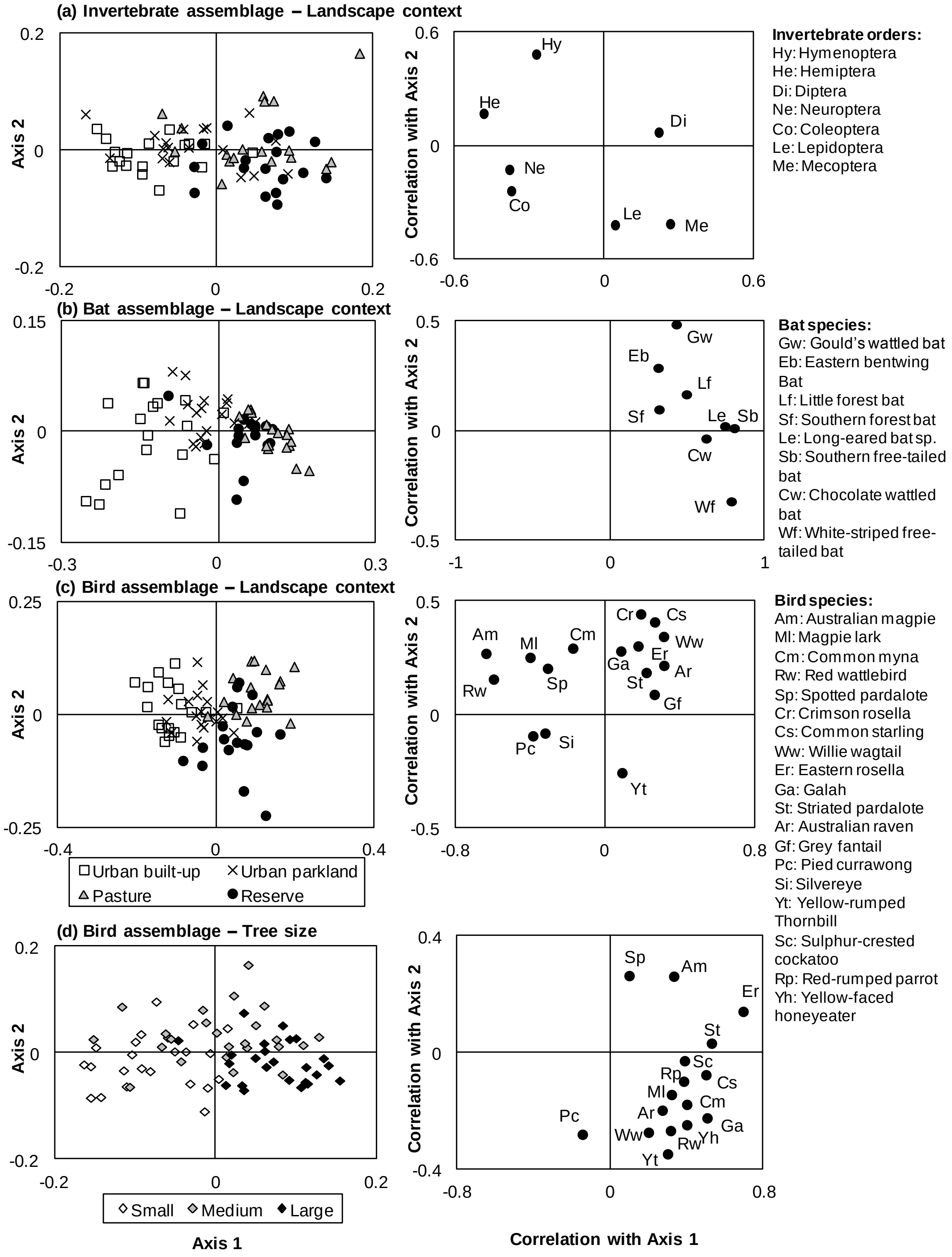


Figure 3. Patterns of variation in wildlife community composition based on significant landscape context and tree size effects. Biplots show: (left panels) constrained multivariate canonical analyses of principal coordinates using discriminant analysis (CAP (CAD)) and; (right panels) corresponding correlations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

Discussion

We tested two hypotheses 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 invertebrates, bats and birds deviated from our ‘landscape context hypothesis’ (Hypothesis 1), which predicted that the highest abundance, richness and most distinct wildlife communities would occur at trees located in reserves (see Fig. 4a for a conceptual model). Instead, wildlife exhibited more complex responses, which underscored the exceptional biodiversity value of scattered trees in modified landscapes. Tree size had a significant effect on birds but did not affect invertebrates and bats. For birds only, this response was consistent with our ‘tree size hypothesis’ (Hypothesis 2; see Fig. 4b). However, trees of all sizes were important for invertebrates and bats. We discuss these findings and their implications for biodiversity conservation.

Hypothesis 1: Effect of landscape context

We found that trees in modified landscapes supported similar invertebrate abundance and richness as trees in reserves (Table 1; Fig. 2a and 2b). This suggests that there are sufficient resources in modified environments to sustain invertebrate populations (Fig. 4a). This is an encouraging result as invertebrate prey availability may facilitate positive bottom-up trophic effects for higher order animals (Ostfeld & Keesing, 2000). We found some evidence to support this as invertebrate abundance at trees had a significant positive effect on bat activity and richness at trees. However, we found significant differences between invertebrate communities at trees in urban built-up areas and reserves. Trees in urban built-up areas supported higher abundance of Coleoptera (beetles), Neuroptera (lacewings), and Hymenoptera (ants, bees and wasps; Fig. 3a), which are ubiquitous orders with many generalist species known to exploit resources in cities (Bang & Faeth, 2011). Trees in reserves supported higher abundance of Diptera (flies), Lepidoptera (moths and butterflies) and Mecoptera (scorpion flies), which may be comprised of more specialist species (e.g. predators and parasites) reliant on resources more readily available in reserves (e.g. carrion; Barton *et al.*, 2013). Conserving trees in a diversity of land-use types will likely benefit a range of invertebrate communities.

Landscape context had a significant effect on 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 (Fig. 2c and 2d). Even for Gould's wattled bat, 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, a species considered sensitive to urbanization, activity was reduced by 85-96% at trees in urban built-up areas. This trend was consistent for all bat species (Fig. 3b) despite similar availability of invertebrate prey at trees across landscape contexts, including prey typically consumed by insectivorous bats (e.g. beetles; Threlfall *et al.*, 2012a). These results suggest that anthropogenic factors in urban built-up areas likely disturb insectivorous bats. Some bat species may be sensitive to artificial light (Threlfall *et al.*, 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). Bats also likely respond to gradients in habitat quality. Activity was concentrated in landscape contexts supporting higher densities of trees (Table S1). Bat activity has been positively correlated with scattered tree density in agricultural (Lumsden & Bennett, 2005) and urban landscapes (Avila-Flores & Fenton, 2005). 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 *et al.*, 2015).

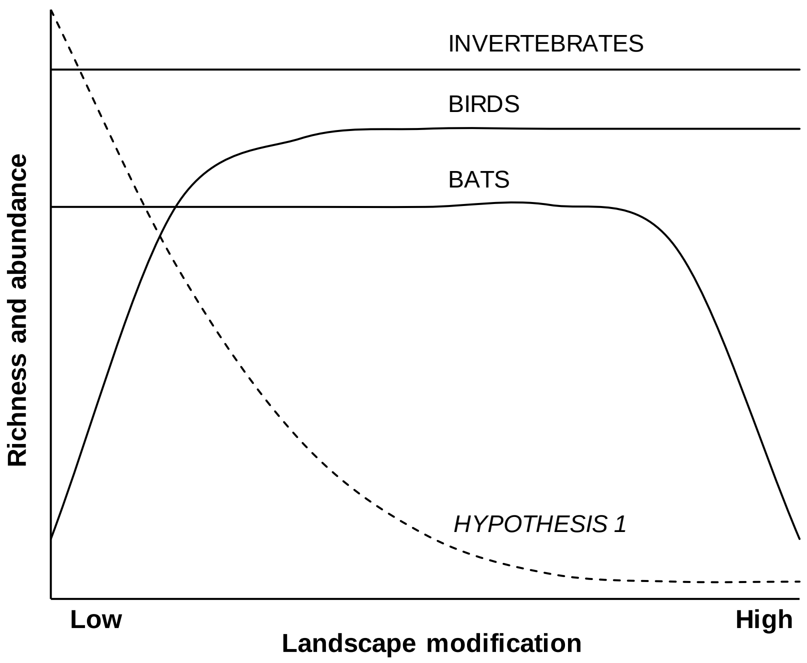
Landscape context had a significant effect on birds. Scattered trees in pasture, urban parklands and urban built-up areas all supported higher bird abundance and species richness than trees in reserves (Fig. 2e and 2f). That is, scattered trees in modified landscapes were disproportionately valuable to birds relative to their availability (Fig. 4a). This response is consistent with a 'diminishing returns model': trees have a higher marginal value for birds inversely proportional to their availability (Cunningham *et al.*, 2014). Isolated trees have previously been shown to serve as important 'life-boats' for birds in hostile environments

(Manning *et al.*, 2004b; DeMars *et al.*, 2010). In reserves, the probability of birds landing at an individual tree is less likely because the value of each tree is essentially ‘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 high biodiversity value of isolated trees. Non-urban and urban trees also supported significantly different bird communities (Fig. 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 *et al.*, 2014b). However, urban trees supported a high abundance of urban-adapted native species (e.g. Australian magpie), which can exploit resources that may be more readily available at trees in urban parklands and urban built-up areas (e.g. canopies for nest construction). 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.*, 2014b).

Hypothesis 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 species compared with medium and small trees. However, this response was pronounced at large scattered trees (Fig. 2e and 2f). 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 (Manning *et al.*, 2012; Le Roux *et al.*, 2014b). Large scattered trees support: complex canopies with dead and living branches important for perching; hollows that are a crucial nesting resources; and large quantities of decorticating bark, flowers and nectar that are important foraging resources (Luck & Daily, 2003; Fischer *et al.*, 2010a; Stagoll *et al.*, 2012). Large trees also supported a more unique bird community compared to medium and small trees (Fig. 3d). A quarter of all species were recorded exclusively at large trees, highlighting that smaller trees alone will not be sufficient to support all bird species (see also Le Roux *et al*., 2015).

(a) Landscape context



(b) Tree size

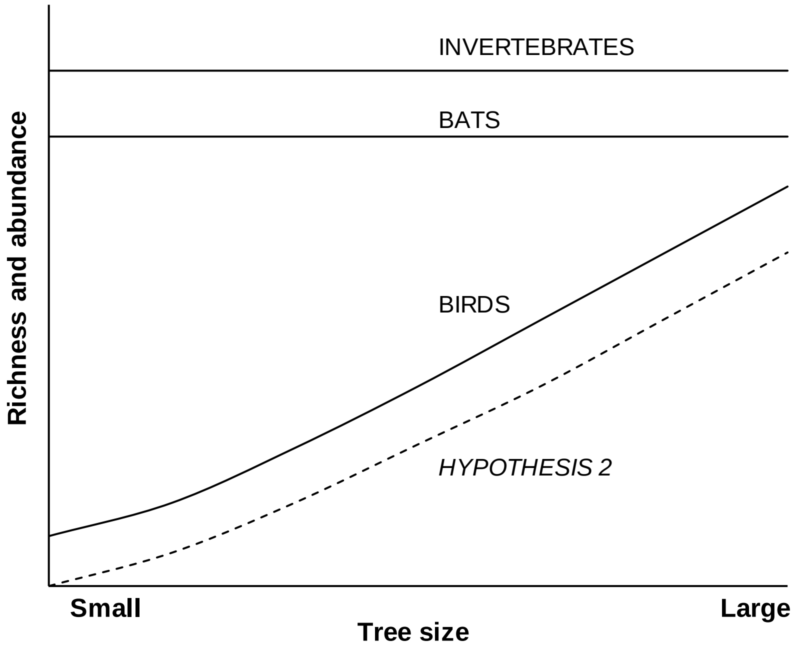


Figure 4. Conceptual models showing variation in wildlife responses quantified at scattered trees: (a) located in different landscape contexts; and (b) of different sizes. Wildlife exhibited complex and contrasting responses that often deviated from tested null hypotheses. Hypotheses were based on the premise that many real-world management practices remain governed by biogeographic principles, resulting in conservation efforts being prioritised in intact and larger habitats. Our results, summarised here, clearly demonstrate that even small isolated scattered trees located in highly disturbed environments offer crucial habitat opportunities for a wide range of animal taxa.

We did not record a significant tree size effect for bats and invertebrates, which may be for two reasons. First, birds likely perceive trees in different ways to bats and invertebrates. Birds are visually orientated and can be selective of tree-level attributes (Manning *et al.*, 2004b). Bird responses were related to tree species but bat responses were related to invertebrate abundance (Table 1). Furthermore, invertebrates exploited trees of all sizes, which may also explain an equivalent bat response (Fig. 4b). Second, tree size effects may not have been detected for bats and invertebrates due to differences in sampling methods. Point count surveys for birds measured direct bird-tree associations. Bat detector surveys and UV invertebrate traps were more indirect sampling approaches.

Implications for biodiversity conservation

We have demonstrated that scattered trees support a rich variety of invertebrate, bat and bird species. Our results emphasise the mismatch between traditional biogeographic predictions and *in situ* animal responses, which defy simplistic theoretical models (Fig. 4). Our results are 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 interact with the landscape as a heterogeneous ‘playing field’ where a range of habitat opportunities exist in different land-use types, which includes exploiting even isolated and small resources like scattered trees. We advocate that there is an urgent need to re-examine land management policies and practices that fail to prioritise the conservation of scattered tree populations on the premise that isolated habitat resources located in hostile environments have limited value for biodiversity (see also Lindenmayer & Franklin, 2002; Manning *et al.*, 2004a; Mendenhall *et al.*, 2014). Semi-natural reserves do play a crucial role in biodiversity conservation and our results also support 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.*, 2014a). Therefore, we strong encourage wildlife-orientated management directives that recognise the exceptional biodiversity value of scattered trees and prioritise tree retention and perpetuation efforts in disturbed environments.

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 (Lindenmayer *et al.*, 2013). For example, strategically planned urban developments could retain more existing trees in urban greenspace rather than removing trees at construction (Stagoll *et al.*, 2012; Le Roux *et al.*, 2014a; Rayner *et al.*, 2014b). Retaining scattered trees can afford immediate habitat benefits to wildlife and may also be a more effective and feasible approach to ameliorate residual development impacts compared to biodiversity offsets like planting many replacement seedlings or purchasing ‘set-aside’ reserve land (Gibbons & Lindenmayer, 2007; Vesk *et al.*, 2008; Maron *et al.*, 2012). In established urban and agricultural landscapes, curtailing ‘tidy-up’ practices at individual trees aimed at removing habitat structures (e.g. pruning dead branches and collecting fallen debris for firewood), could further increase habitat opportunities for wildlife (Manning *et al.*, 2006; Carpaneto *et al.*, 2010; Le Roux *et al.*, 2014b). Furthermore, scattered trees can serve as useful structure-based indicators of biodiversity (Lindenmayer *et al.*, 2000; Tews *et al.*, 2004). That is, conserving trees in disturbed landscapes maintains high levels of biodiversity and ongoing removal of trees, even in highly disturbed landscapes, is likely to result in the loss of not only biological diversity but also vital ecological services (e.g. pollination and seed dispersal; Herrera & García, 2009).

Our results also highlight the importance of large old trees, especially for birds (see also Stagoll *et al.*, 2012; Barth *et al.*, 2015). Other taxa are likely to benefit from resources provided only by large trees, such as hollows for roosting bats and dead limbs for sheltering invertebrates (Lumsden *et al.*, 2002; Jonsell, 2012). These structures form over centuries and once removed are irreplaceable in the short-term (Manning *et al.*, 2012). However, our results also revealed the biodiversity value of smaller sized trees, which should not be discounted. Tree management policies that afford protection only to large scattered trees should be broadened to also include medium and small trees. Maintaining a range of tree sizes in modified landscapes is crucial for the long-term perpetuation of large trees (Gibbons *et al.*, 2008; Le Roux *et al.*, 2014a).

Effective biodiversity conservation requires integrating wildlife response data into targeted management and habitat protection policies implemented at multiple spatial scales. To better align conservation priorities for different taxa in modified landscapes we recommend: (1) planning for mosaics of different land-use types; and (2) prioritising the protection, retention and perpetuation of scattered trees of different sizes. These strategies can provide crucial habitat benefits to a multitude of species in modified landscapes.

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Supporting information

Table S1 Summary of landscape attributes measured at sample trees in each landscape context (*n* = 18). Means ± SEM are provided. Percentage cover of select features were calculated in ArcGis (esri, 2010) using Object Based Image Analysis (OBIA) at 50 m and 250 m radius buffers with all sample trees (n = 72) held at the centre.

Attributes	**Landscape context**			
	Reserve	Pasture	Urban parkland	Urban built-up
Distance to nearest tree (m)	6.8 ± 0.9	26.5 ± 5.6	12.9 ± 1.6	23.9 ± 4.1
Tree density (0.1 ha plot)	56.9 ± 9.9	13.3 ± 5.6	16.1 ± 4.4	1.8 ± 0.3
50 m buffer				
% trees	38.6 ± 7.1	17.3 ± 4.2	32.9 ± 4.4	29.4 ± 4.1
% grass	45.2 ± 5.8	72.6 ± 5.3	44.3 ± 3.9	26.8 ± 1.2
% roads and buildings	7.1 ± 2.6	0.0 ± 0.0	15.8 ± 2.6	34.5 ± 2.9
250 m buffer				
% trees	37.5 ± 6.6	14.3 ± 2.1	28.8 ± 4.2	27.1 ± 3.3
% grass	41.2 ± 4.8	76.2 ± 3.3	31.2 ± 3.8	30.1 ± 1.2
% roads and buildings	11.2 ± 3.7	1.1 ± 0.3	29.8 ± 2.3	34.3 ± 2.2

Table S2 Summary of structural attributes measured at sample trees (n = 72) of varying sizes situated in different landscape contexts (n = 6). Means ± SEM are provided.

Attributes	**Tree size category**	**Landscape context**			
		Reserve	Pasture	Urban parkland	Urban built-up
Diameter at breast height (DBH, cm)	Small (20-50 cm DBH)	33.8 ± 2.7	37.3 ± 1.9	37.8 ± 2.1	41.6 ± 2.5
	Medium (51-80 cm)	60.0 ± 3.2	63.3 ± 3.2	66.6 ± 3.9	71.2 ± 2.7
	Large (> 80 cm)	105.8 ± 7.4	116.5 ± 12.9	122.0 ± 8.2	104.5 ± 6.8
Height (m)	S	11.3 ± 0.8	9.4 ± 0.8	14.3 ± 1.6	14.5 ± 1.2
	M	19.3 ± 2.4	13.9 ± 1.4	15.8 ± 1.5	17.9 ± 1.1
	L	18.1 ± 2.6	19.7 ± 1.3	21.9 ± 1.1	23.7 ± 1.8
Canopy width (m)	S	7.4 ± 0.5	8.3 ± 0.9	10.8 ± 1.6	12.1 ± 1.2
	M	13.5 ± 0.9	12.5 ± 1.6	15.3 ±0.9	15.6 ± 1.6
	L	18.0 ± 1.3	21.5 ± 1.7	21.8 ± 1.1	21.5 ± 1.8
Number of epiphytes	S	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	M	0.5 ± 0.3	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
	L	4.3 ± 1.4	3.6 ± 3.2	0.2 ± 0.2	0.0 ± 0.0
Number of hollows	S	0.0 ± 0.0	0.6 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
	M	1.5 ± 0.9	1.6 ± 0.5	0.0 ± 0.0	1.0 ± 0.6
	L	2.8 ± 1.0	5.7 ± 3.1	5.6 ± 3.0	0.0 ± 0.0
Number of fallen logs (> 10 cm DBH, 10 m radius of tree)	S	0.3 ± 0.3	2.3 ± 1.5	0.2 ± 0.2	0.0 ± 0.0
	M	2.0 ± 0.6	1.0 ± 0.5	0.0 ± 0.0	0.0 ± 0.0
	L	5.8 ± 2.9	5.6 ± 3.1	0.7 ± 0.4	0.0 ± 0.0
% of peeling bark cover on limbs	S	9.6 ± 4.1	3.2 ± 2.4	4.6 ± 3.1	1.8 ± 0.7
	M	6.3 ± 2.1	3.3 ± 2.1	4.0 ± 2.3	5.5 ± 2.3
	L	12.8 ± 4.7	9.5 ± 2.8	14.5 ± 6.5	12.5 ± 3.8
% of dead branches in canopy	S	2.6 ± 1.5	9.5 ± 7.3	5.1 ± 3.9	1.6 ± 0.3
	M	18.6 ± 7.1	17.6 ± 6.9	8.1 ± 2.4	13.8 ± 5.1
	L	39.1 ± 10.1	24.5 ± 5.5	14.5 ± 3.2	7.1 ± 2.2
% of litter cover (10 m radius of tree)	S	30.0 ± 9.1	14.6 ± 6.1	13.6 ± 3.6	23.5 ± 8.5
	M	35.0 ± 10.3	10.0 ± 2.5	9.1 ± 3.9	12.0 ± 6.3
	L	27.0 ± 9.4	11.1 ± 3.0	11.3 ± 6.2	11.6 ± 4.6

Table S3. A summary of the invertebrate orders, bat species and bird species recorded in different landscape contexts (R-reserve, P-pasture, UP-urban parklands, UB-urban built-up) and at different tree sizes (S-small, M-medium, L-large). The total abundance or relative activity (i.e. number of invertebrates caught, number of bat passes recorded and number of birds recorded) are presented for each taxon. Introduced species are denoted by an asterisk.

Common name	**Scientific name**	**Landscape context**	**Tree size**	**Total abundance / relative activity**
Invertebrate orders				**47,096**
Spiders, scorpions, ticks	Arachnida	R, P, UP, UB	S, M, L	330
Cockroaches	Blattodae	R, P, UP, UB	S, M, L	30
Beetles	Coleoptera	R, P, UP, UB	S, M, L	7,348
Earwigs	Dermaptera	P, UP, UB	S, M, L	66
Flies	Diptera	R, P, UP, UB	S, M, L	16,362
Mayflies	Ephemeroptera	UP	M	1
True bugs	Hemiptera	R, P, UP, UB	S, M, L	467
Bees, wasps, ants	Hymenoptera	R, P, UP, UB	S, M, L	5,214
Isopods	Isopoda	R, P, UP, UB	S, M, L	20
Moths, butterflies	Lepidoptera	R, P, UP, UB	S, M, L	15,687
Mantids	Mantadea	R, P, UP, UB	S, M, L	6
Scorpion flies	Mecoptera	R, P, UP, UB	S, M, L	796
Snails, slugs	Mollusca	UB	M	20
Centipedes, millipedes	Myriapoda	R, UP, UB	M, L	6

Lacewings	Neuroptera	R, P, UP, UB	S, M, L	643
Dragonflies	Odonata	R, P, UP	S, L	11
Crickets	Orthoptera	R, P, UP, UB	S, M, L	14
Stoneflies	Plecoptera	R	M	1
Caddisflies	Tricoptera	R, P, UP, UB	S, M, L	74
Bat species				**30,536**
Chocolate wattled bat	*Chalinolobus morio*	R, P, UP, UB	S, M, L	1,747
Eastern false pipistrelle	*Falsistrellus tasmaniensis*	R	S, M, L	6
Eastern bent-wing bat	*Miniopterus schreibersii oceanensis*	R, P, UP, UB	S, M, L	1,687
Gould’s wattled bat	*Chalinolobus gouldii*	R, P, UP, UB	S, M, L	17,795
Large forest bat	*Vespadelus darlingtoni*	R, P, UP, UB	S, M, L	1,561
Little forest bat	*Vespadelus vulturnus*	R, P, UP, UB	S, M, L	1,724
Long-eared bat spp.	*Nyctophilus gouldi* / *Nyctophilus geoffroyi* (species complex)	R, P, UP, UB	S, M, L	372
Southern forest bat	*Vespadelus regulus*	R, P, UP, UB	S, M, L	1,298
Southern free-tailed bat	*Mormopterus planiceps* (sp4)	R, P, UP, UB	S, M, L	2,138
White-striped free-tailed bat	*Tadarida australis*	R, P, UP, UB	S, M, L	2,203
Yellow-bellied sheath-tailed bat	*Saccolaimus flaviventris*	R	S	5

Bird species				**1,785**
Australian king parrot	*Alisterus scapularis*	UP	S, M, L	13
Australian magpie	*Cracticus tibicen*	R, P, UP, UB	S, M, L	143
Australian raven	*Corvus coronoides*	R, P	S, M, L	14
Australian Wood-duck	*Chenonetta jubata*	P	L	1
Black-faced cuckoo-shrike	*Coracina novaehollandiae*	R, P	S, M, L	11
Brown falcon	*Falco berigora*	P	L	2
Brown thornbill	*Acanthiza pusilla*	R	S, L	5
Buff-rumped thornbill	*Acanthiza reguloides*	R, P, UB	S, M, L	21
Common blackbird*	*Turdus merula*	UP, UB	M, L	4
Common myna*	*Acridotheres tristis*	P, UP, UB	M, L	60
Common starling*	*Sturnus vulgaris*	P, UP, UB	M, L	150
Crested pigeon	*Ocyphaps lophotes*	P, UP, UB	S, M, L	5
Crimson rosella	*Platycercus elegans*	R, P, UP, UB	S, M, L	143
Dusky woodswallow	*Artamus cyanopterus*	P	M	2
Eastern rosella	*Platycercus eximius*	R, P, UP, UB	S, M, L	216
Eastern yellow robin	*Eopsaltria australis*	P, UP	S, M	3
Flame robin	*Petroica phoenicea*	P, UP	M, L	2
Fuscous honeyeater	*Lichenostomus fuscus*	P	L	6

Galah	*Cacatua roseicapilla*	R, P, UP, UB	S, M, L	59
Gang-gang cockatoo	*Callocephalon fimbriatum*	R	M	2
Golden whistler	*Pachycephala pectoralis*	P, UB	S, M, L	6
Grey butcherbird	*Cracticus torquatus*	R, P	L, M	3
Grey fantail	*Rhipidura fuliginosa*	R, P, UP, UB	S, M, L	30
Grey shrike-thrush	*Colluricincla harmonica*	P	L	1
Jacky winter	*Microeca fascinans*	R	S	2
House sparrow*	*Passer domesticus*	UP, UB	M, L	8
Laughing kookaburra	*Dacelo novaeguineae*	UP	L	2
Little corella	*Cacatua sanguinea*	P, UP	M, L	9
Magpie-lark	*Grallina cyanoleuca*	R, P, UP, UB	S, M, L	48
Mistletoebird	*Dicaeum hirundinaceum*	R, P, UP	L	5
Noisy friarbird	*Philemon corniculatus*	P, UP, UB	S, M, L	32
Noisy miner	*Manorina melanocephala*	R, P, UP, UB	S, M, L	83
Olive-backed oriole	*Oriolus sagittatus*	P	L	1
Pied currawong	*Strepera graculina*	R, P, UP, UB	S, M, L	77
Red wattlebird	*Anthochaera carunculata*	R, P, UP, UB	S, M, L	121
Red-browed finch	*Neochmia temporalis*	P	M	2
Red-rumped parrot	*Psephotus haematonotus*	R, P, UP, UB	M, L	28

Rufous whistler	*Pachycephala rufiventris*	R, UP	M	2
Sacred kingfisher	*Todiramphus sanctus*	P	M	1
Satin flycatcher	*Myriagra cyanoleuca*	P	L	2
Scarlet robin	*Petroica multicolour*	P	L	1
Silvereye	*Zosterops lateralis*	R, UP, UB	S, M, L	73
Speckled warbler	*Chthonicola sagittata*	UB	M	1
Spotted pardalote	*Pardalotus punctatus*	R, P, UP, UB	S, M, L	23
Striated pardalote	*Pardalotus striatus*	R, P, UP, UB	S, M, L	100
Sulphur-crested cockatoo	*Cacatua galerita*	R, P, UP, UB	M, L	23
Superb fairy-wren	*Malurus cyaneus*	P	M	5
Superb parrot	*Polytelis swainsonii*	UP	L	6
Tree martin	*Hirundo nigricans*	P	M, L	4
Varied sittella	*Daphoenositta chrysoptera*	R	L	1
Weebill	*Smicrornis brevirostris*	R, P, UP, UB	S, M, L	34
Welcome swallow	*Hirundo neoxena*	UP	L	1
Western gerygone	*Gerygone fusca*	P	L	1
White-naped honeyeater	*Melithreptus lunatus*	P	L	3
White-plumed honeyeater	*Lichenostomus penicillatus*	R, P	M, L	21
White-throated gerygone	*Gerygone olivacea*	R	L	1

White-winged choughs	*Corcorax melanorhamphos*	UP	S	3
Willie wagtail	*Rhipidura leucophrys*	R, P	M, L	9
Yellow thornbill	*Acanthiza nana*	P	L	3
Yellow-faced honeyeater	*Lichenostomus chysops*	R, P, UP, UB	S, M, L	114
Yellow-rumped thornbill	*Acanthiza chrysorrhoa*	R, P, UP, UB	S, M, L	33

Table S4 Generalized linear mixed regression model (GLMM) summary results for six wildlife response variables, including: invertebrate abundance and richness; bat activity and richness; and bird abundance and richness. For abundance (activity) and richness data we fitted normal distributions (identity link) and Poisson (log-link) distributions, respectively. Reference levels for landscape context (reserve) and tree size (small) were held at zero.

Response	**Fixed effects**		**Wald statistic**	**d.f.**	**Parameter estimate**	**Standard error (average)**	***p*-value**
Invertebrate abundance	(Residual variance model)				0.68	0.08	
	(Intercept)				5.17	0.33	
	Landscape context		0.86	3			0.835
		Reserve			0.00	(0.34)	
		Pasture			-0.64		
		Urban parkland			0.12		
		Urban built-up			-0.09		
	Tree size		2.08	2			0.360
		Small			0.00	(0.33)	
		Medium			0.02		
		Large			0.01		
	Landscape context*Tree size		10.89	6			0.112
	Tree species		2.11	2			0.355
Invertebrate richness	(Residual variance model)				0.33	0.04	
	(Intercept)				1.89	0.09	
	Landscape context		5.25	3			0.167
		Reserve			0.00	(0.08)	
		Pasture			-0.08		
		Urban parkland			-0.01		
		Urban built-up			0.12		
	Tree size		1.25	2			0.539
		Small			0.00	(0.07)	
		Medium			0.02		
		Large			-0.02		
	Landscape context*Tree size		3.87	6			0.693
	Tree species		3.19	2			0.212

Bat activity	(Residual variance model)				0.80	0.09	
	(Intercept)				4.47	0.43	
	Landscape context		35.12	3			<0.001
		Reserve			0.00	(0.44)	
		Pasture			0.55		
		Urban parkland			-0.15		
		Urban built-up			-1.05		
	Tree size		0.34	2			0.845
		Small			0.00	(0.43)	
		Medium			-0.15		
		Large			0.38		
	Landscape context*Tree size		6.06	6			0.427
	Tree species		0.19	2			0.912
	Invertebrate abundance / tree		10.32	1			0.002
Bat richness	Residual variance model				0.43	0.05	
	Intercept				1.87	0.09	
	Landscape context		65.31	3			<0.001
		Reserve			0.00	(0.13)	
		Pasture			0.12		
		Urban parkland			-0.15		
		Urban built-up			-0.66		
	Tree size		1.31	2			0.523
		Small			0.00	(0.12)	
		Medium			-0.11		
		Large			0.10		
	Landscape context*Tree size		9.81	6			0.155
	Tree species		0.02	2			0.989
	Invertebrate abundance / tree		7.68	1			0.006
Bird abundance	Residual variance model				0.65	0.08	
	Intercept				0.79	0.23	
	Landscape context		29.81	3			< 0.001
		Reserve			0.00	(0.31)	
		Pasture			0.07		

		Urban parkland			0.49		
		Urban built-up			0.80		
	Tree size		97.55	2			< 0.001
		Small			0.00	(0.29)	
		Medium			0.42		
		Large			1.25		
	Landscape context*Tree size		14.28	6			0.040
	Tree species		11.40	2			0.005
	Invertebrate abundance / tree		1.69	1			0.196
Bird richness	Residual variance model				1.03	0.12	
	Intercept				-0.22	0.33	
	Landscape context		10.23	3			0.024
		Reserve			0.00	(0.37)	
		Pasture			0.33		
		Urban parkland			0.83		
		Urban built-up			0.84		
	Tree size		76.14	2			< 0.001
		Small			0.00	(0.35)	
		Medium			0.80		
		Large			1.64		
	Landscape context*Tree size		8.29	6			0.235
	Tree species		8.07	2			0.023
	Invertebrate abundance / tree		1.12	1			0.293

Table S5. Permutational multivariate analysis of variance (PERMANOVA) testing differences between invertebrate, bat and bird communities recorded at trees located in different landscape contexts and at trees of different sizes. Only significant pair-wise comparisons are shown.

Response		**Fixed effects**		
		Landscape context	Tree size	Landscape context*Tree size
Invertebrate assemblage	d.f.	3	2	6
	F-ratio	1.84	0.79	1.05
	p-value	0.038	0.635	0.397
	Groups:	*p*-value	*t*-statistic	
	Reserve vs. urban built-up	0.008	1.88	
Bat assemblage	d.f.	3	2	6
	F-ratio	9.21	0.60	0.97
	p-value	< 0.001	0.780	0.969
	Groups:	*p*-value	*t*-statistic	
	Reserve vs. urban built-up	< 0.001	3.44	
	Pasture vs. urban built-up	< 0.001	4.82	
	Urban parkland vs. urban built-up	< 0.001	2.67	
Bird assemblage	d.f.	3	2	6
	F-ratio	2.83	3.05	1.04
	p-value	< 0.001	< 0.001	0.384
	Groups:	*p*-value	*t*-statistic	
	Reserve vs. urban parkland	< 0.001	1.56	
	Reserve vs. urban built-up	< 0.001	1.71	
	Pasture vs. urban parkland	< 0.001	1.63	
	Pasture vs. urban built-up	< 0.001	2.35	
	Small vs. medium	0.014	1.43	
	Small vs. large	< 0.001	2.13	
	Medium vs. large	0.026	1.35	

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

In Paper III, I demonstrated that scattered trees are used by a diverse range of animal species, which suggests that conventional land management and conservation priorities that ‘triage’ isolated and small habitat resources may need to be re-evaluated. In Paper IV, I used the premise of the SLOSS (single large or several small) debate to determine whether many smaller trees are a valid biodiversity offset for the loss of a single large tree.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2015). Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets. *Biological Conservation*, 191, 558-566.

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.

Keywords Birds; island biogeography theory; large old trees; landscape modification; no net loss; SLOSS

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 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 (Millenium 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).

Materials and methods

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).

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 km^2. 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).

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 am, avoiding unfavourable weather.

Data analyses

1. Basal area analysis

We calculated tree basal area from DBH measurements for all sample trees (0.00007854 x DBH^2; Husch et al., 1993). Hence, tree sizes included: small (0.05-0.19 m^2), medium (0.20-0.49 m^2) and large trees (0.50-2.30 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. 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).

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 (5.14-7.12 m^2) compared with medium (1.72-2.40 m^2) and small tree samples (0.56-0.83 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.

Results

We recorded 1,188 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%).

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 x 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 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.

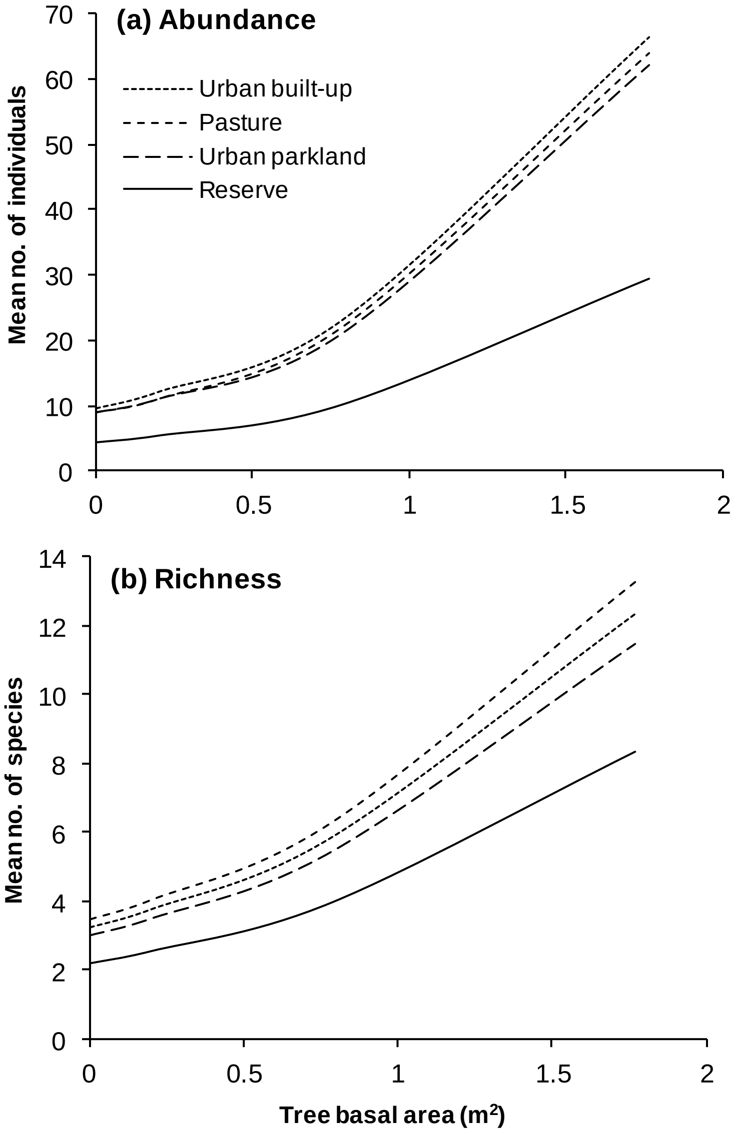

Figure 1. Predicted relationships between tree basal area (m^2) and bird abundance (a) and species richness (b) in different landscape contexts (reserves, pasture, urban parklands and urban built-up areas). Basal areas indicated on the *x*-axes, 0, 0.5, 1, 1.5 and 2, correspond approximately to the following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

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 (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).

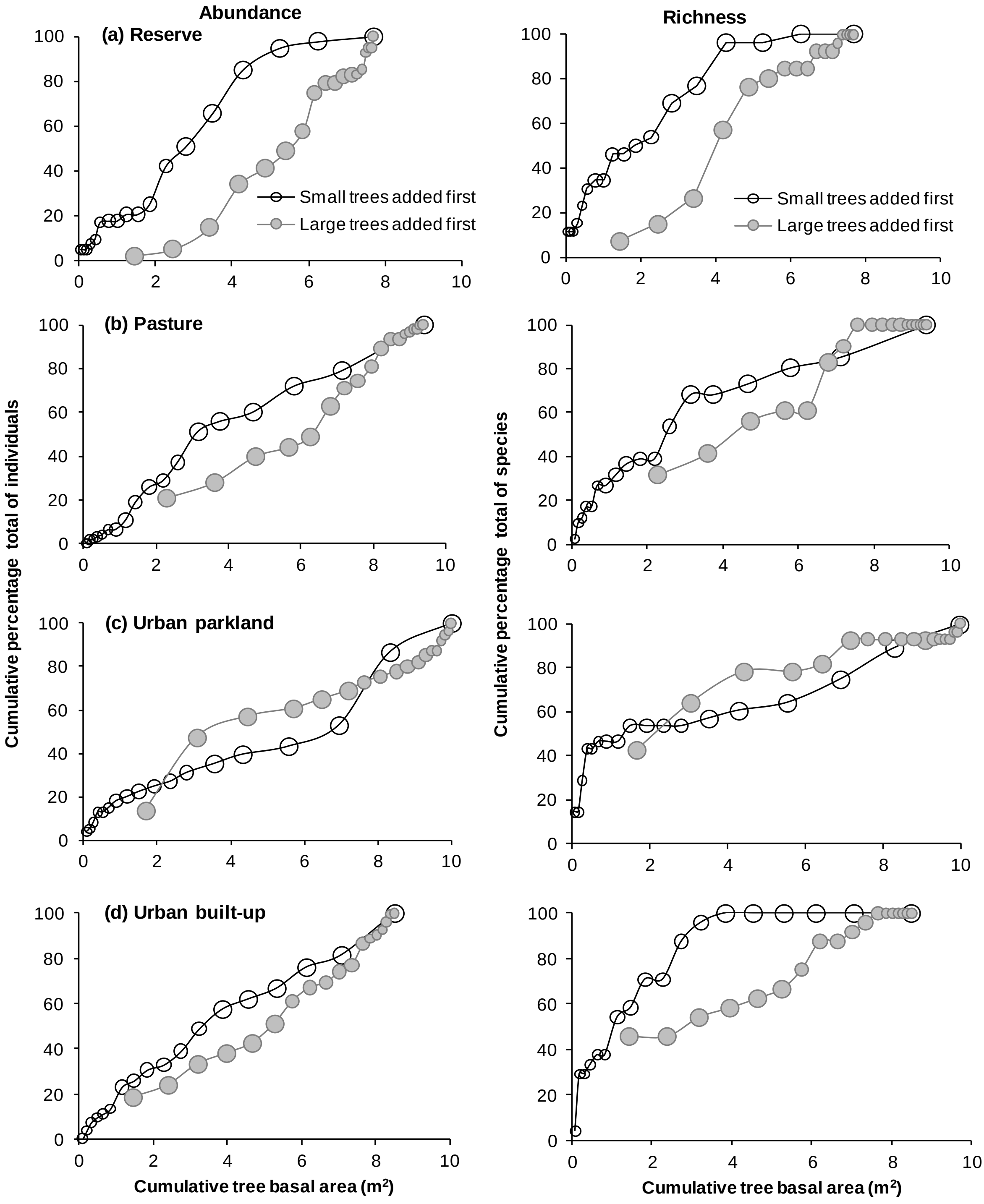

Figure 2. Cumulative percentage total of individuals (abundance) and species (richness) plotted against the cumulative tree basal area (m^2) of sampled trees in each landscape context, including: reserves (a), pasture (b), urban parkland (c) and urban built-up areas (d). Plotted data represents the sequential 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; 0.05-0.19 m^2 basal area; smallest markers), medium trees (51-80 cm; 0.20-0.49 m^2; medium sized markers) and large trees (> 80 cm; 0.50-2.30 m^2; largest markers).

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 where 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.

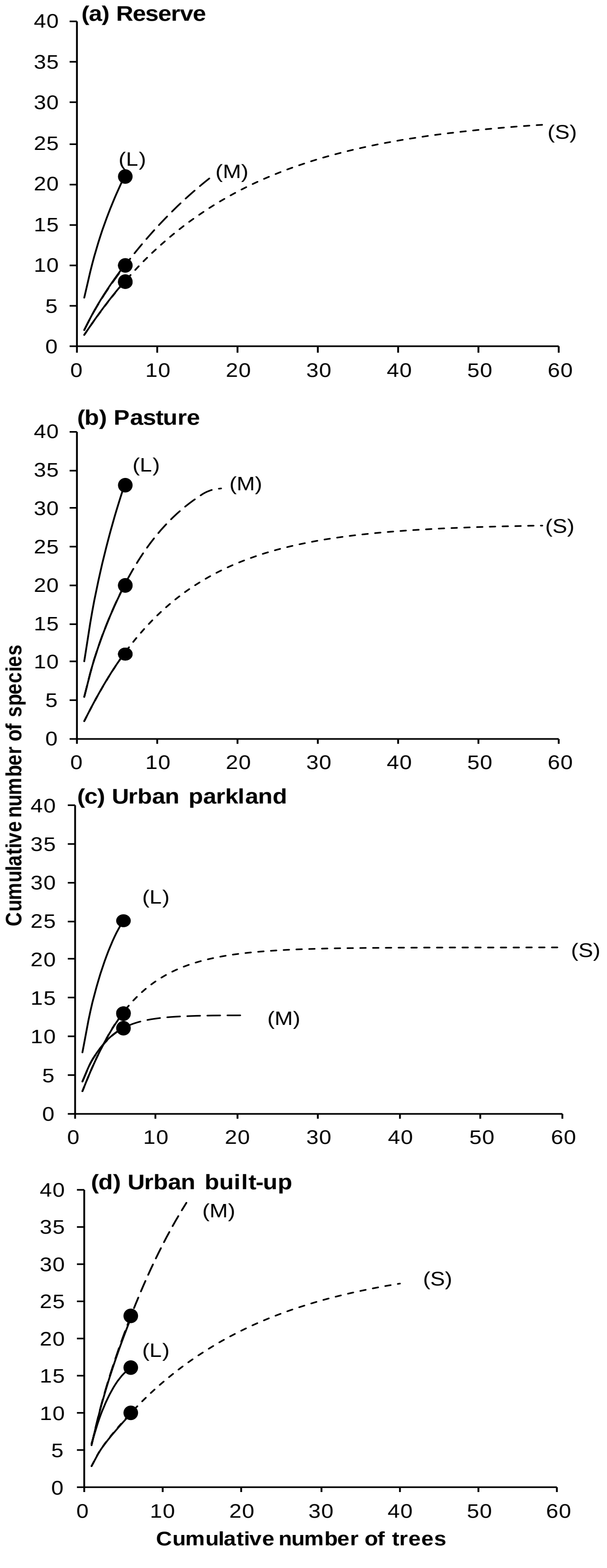

Figure 3. Sample-based rarefaction curves for birds at trees of different sizes (small trees (20-50 cm DBH; 0.05-0.19 m^2 basal area; (S)), medium trees (51-80 cm; 0.20-0.49 m^2; (M)) and large trees (> 80 cm; 0.50-2.30 m^2; (L)) located in different landscape contexts, including: reserves (a), pasture (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 m^2 basal area) or medium trees (51-80 cm; 0.20-0.49 m^2) needed to support an equivalent mean number of individual birds (abundance), bird species (richness) and basal area habitat (m^2) as a single large tree (> 80 cm; 0.50-2.30 m^2) 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
Small trees:				
Abundance	4	10	5	4
Richness	4	5	3	2
Basal area	10	10	11	6
Medium trees:				
Abundance	2	2	4	1
Richness	3	2	2	1
Basal area	3	4	3	2

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.

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 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.

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 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; Katoh 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).

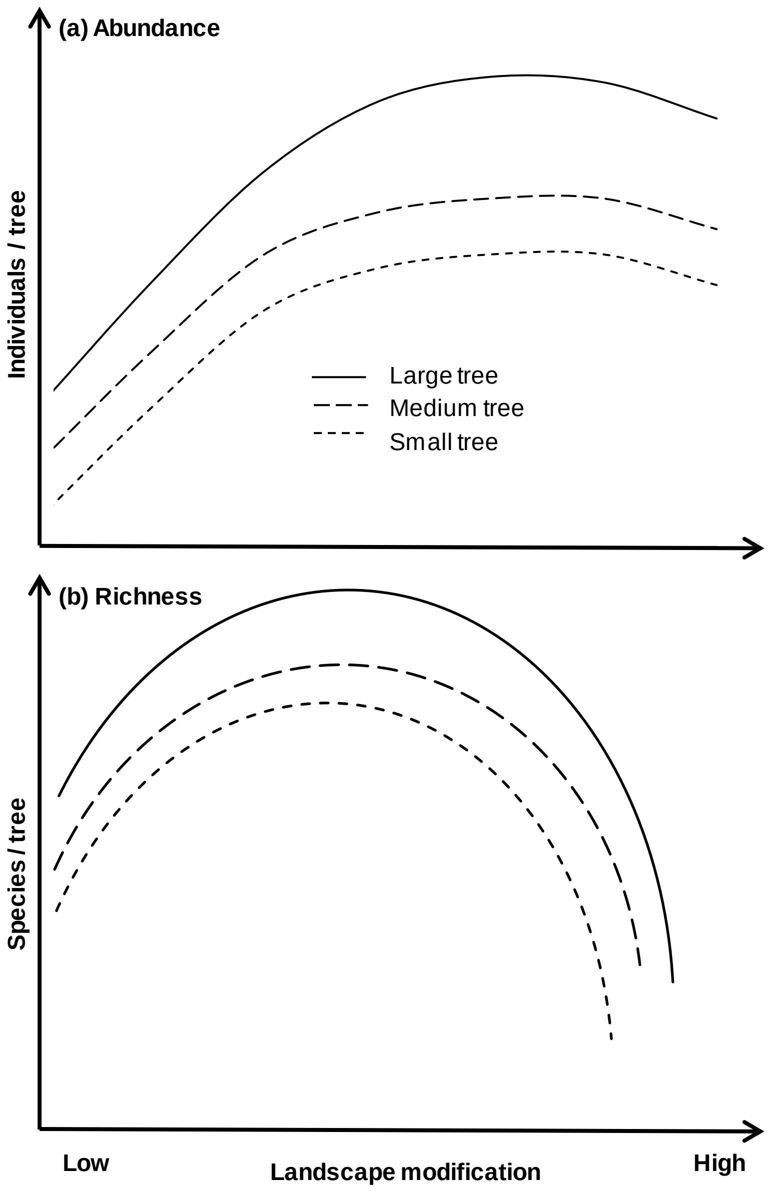

Figure 4. Conceptual models showing bird responses at trees of different sizes located in landscape contexts with varying degrees of modification. Bird abundance (a) deviated from habitat-isolation predictions as more individuals were associated with trees located in modified landscapes (pasture, urban 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.

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.

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; Vesk 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 (< 10cm DBH) as the only habitat compensation, which may not even be suitable tree equivalents.

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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Supporting information

Table A1 Summary of landscape attributes (means ± SEM) measured at sample trees (n = 18) in different landscape contexts (reserve, pasture, urban parklands and urban built-up areas). Percentage cover of select features were calculated in ArcGis (esri, 2010) using Object Image Analysis (OBIA) at 50 m and 250 m radius buffers with sample trees (n = 72) held as the centre point.

Attributes	Landscape context			
	Reserve	Pasture	Urban parkland	Urban built-up
Distance to nearest tree (m)	6.8 ± 0.9	26.5 ± 5.6	12.9 ± 1.6	23.9 ± 4.1
Tree density (0.1 ha plot)	56.9 ± 9.9	13.3 ± 5.6	16.1 ± 4.4	1.8 ± 0.3
50 m buffer				
% trees	38.6 ± 7.1	17.3 ± 4.2	32.9 ± 4.4	29.4 ± 4.1
% grass	45.2 ± 5.8	72.6 ± 5.3	44.3 ± 3.9	26.8 ± 1.2
% roads and buildings	7.1 ± 2.6	0.0 ± 0.0	15.8 ± 2.6	34.5 ± 2.9
250 m buffer				
% trees	37.5 ± 6.6	14.3 ± 2.1	28.8 ± 4.2	27.1 ± 3.3
% grass	41.2 ± 4.8	76.2 ± 3.3	31.2 ± 3.8	30.1 ± 1.2
% roads and buildings	11.2 ± 3.7	1.1 ± 0.3	29.8 ± 2.3	34.3 ± 2.2

Table A2 Summary of structural attributes (means ± SEM) measured at sample trees (n = 72) of different sizes (small (20-50 cm DBH; 0.05-0.19 m^2 basal area), medium (51-80 cm; 0.20-0.49 m^2), and large (> 80 cm; 0.50-2.30 m^2)) located in different landscape contexts (reserve, pasture, urban parklands and urban built-up areas).

Attributes	Tree size category	Landscape context			
		Reserve	Pasture	Urban parkland	Urban built-up
Diameter at breast height (DBH, cm)	Small	33.8 ± 2.7	37.3 ± 1.9	37.8 ± 2.1	41.6 ± 2.5
	Medium	60.0 ± 3.2	63.3 ± 3.2	66.6 ± 3.9	71.2 ± 2.7
	Large	105.8 ± 7.4	116.5 ± 12.9	122.0 ± 8.2	104.5 ± 6.8
Height (m)	S	11.3 ± 0.8	9.4 ± 0.8	14.3 ± 1.6	14.5 ± 1.2
	M	19.3 ± 2.4	13.9 ± 1.4	15.8 ± 1.5	17.9 ± 1.1
	L	18.1 ± 2.6	19.7 ± 1.3	21.9 ± 1.1	23.7 ± 1.8
Canopy width (m)	S	7.4 ± 0.5	8.3 ± 0.9	10.8 ± 1.6	12.1 ± 1.2
	M	13.5 ± 0.9	12.5 ± 1.6	15.3 ±0.9	15.6 ± 1.6
	L	18.0 ± 1.3	21.5 ± 1.7	21.8 ± 1.1	21.5 ± 1.8
Number of epiphytes	S	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	M	0.5 ± 0.3	0.3 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
	L	4.3 ± 1.4	3.6 ± 3.2	0.2 ± 0.2	0.0 ± 0.0
Number of hollows	S	0.0 ± 0.0	0.6 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
	M	1.5 ± 0.9	1.6 ± 0.5	0.0 ± 0.0	1.0 ± 0.6
	L	2.8 ± 1.0	5.7 ± 3.1	5.6 ± 3.0	0.0 ± 0.0
Number of fallen logs (> 10 cm DBH, 10 m radius of tree)	S	0.3 ± 0.3	2.3 ± 1.5	0.2 ± 0.2	0.0 ± 0.0
	M	2.0 ± 0.6	1.0 ± 0.5	0.0 ± 0.0	0.0 ± 0.0
	L	5.8 ± 2.9	5.6 ± 3.1	0.7 ± 0.4	0.0 ± 0.0
% of peeling bark cover on trunk/limbs	S	9.6 ± 4.1	3.2 ± 2.4	4.6 ± 3.1	1.8 ± 0.7
	M	6.3 ± 2.1	3.3 ± 2.1	4.0 ± 2.3	5.5 ± 2.3
	L	12.8 ± 4.7	9.5 ± 2.8	14.5 ± 6.5	12.5 ± 3.8
% of dead branches in canopy	S	2.6 ± 1.5	9.5 ± 7.3	5.1 ± 3.9	1.6 ± 0.3
	M	18.6 ± 7.1	17.6 ± 6.9	8.1 ± 2.4	13.8 ± 5.1
	L	39.1 ± 10.1	24.5 ± 5.5	14.5 ± 3.2	7.1 ± 2.2
% of litter cover (10 m radius of tree)	S	30.0 ± 9.1	14.6 ± 6.1	13.6 ± 3.6	23.5 ± 8.5
	M	35.0 ± 10.3	10.0 ± 2.5	9.1 ± 3.9	12.0 ± 6.3
	L	27.0 ± 9.4	11.1 ± 3.0	11.3 ± 6.2	11.6 ± 4.6

Table A3. List of recorded bird species. Bird habitat, nesting and foraging guilds are provided along with the landscape contexts (reserve (R), pasture (P), urban parkland (UP) and urban built-up areas (UB)) and tree sizes (small (20-50 cm DBH; 0.05-0.19 m^2 basal area; S), medium (51-80 cm; 0.20-0.49 m^2; M) and large (> 80 cm; 0.50-2.30 m^2; L)) where birds were recorded at. Species only recorded at large trees are indicated with an asterisk.

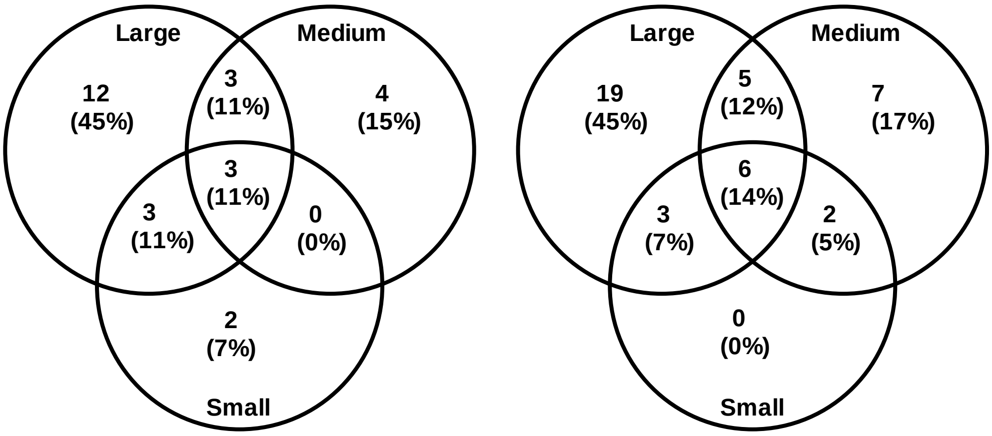
Common name	Scientific name	Woodland status	Nesting guild	Foraging guild	Landscape context	Tree size	Total individuals
Australian king parrot	*Alisterus scapularis*	Woodland generalist (WG)	Hollow-nester (H)	Granivore (G)	UP	S, M, L	13
Australian magpie	*Cracticus tibicen*	WG	Arboreal-nester (A)	Insectivore (I)	R, P, UP, UB	S, M, L	84
Australian raven	*Corvus coronoides*	WG	A	I	R, P	S, M, L	12
Australian Wood-duck*	*Chenonetta jubata*	WG	H	Other (O)	P	L	1
Black-faced cuckoo-shrike	*Coracina novaehollandiae*	Woodland specialist (WS)	A	I	R, P	S, M, L	6
Brown thornbill	*Acanthiza pusilla*	WS	Understorey (U)	I	R	S, L	7
Buff-rumped thornbill	*Acanthiza reguloides*	WS	U	I	R, P, UB	S, M, L	18
Common blackbird (introduced)	*Turdus merula*	WG	U	I	UB	M	1
Common myna (introduced)	*Acridotheres tristis*	WG	H	I	P, UP, UB	M, L	44
Common starling	*Sturnus vulgaris*	WG	H	I	P, UP, UB	M, L	88

(introduced)							
Crested pigeon	*Ocyphaps lophotes*	WG	A	G	P, UP, UB	S, M, L	5
Crimson rosella	*Platycercus elegans*	WS	H	G	R, P, UP, UB	S, M, L	105
Dusky woodswallow	*Artamus cyanopterus*	WS	Opportunistic (O)	I	P	M	2
Eastern rosella	*Platycercus eximius*	WS	H	G	R, P, UP, UB	S, M, L	138
Flame robin*	*Petroica phoenicea*	WS	U	I	P	L	1
Fuscous honeyeater*	*Lichenostomus fuscus*	WS	U	Nectar (N)	P	L	6
Galah	*Cacatua roseicapilla*	WG	H	G	R, P, UP	M, L	26
Golden whistler	*Pachycephala pectoralis*	WS	U	I	P, UB	S, M, L	6
Grey butcherbird	*Cracticus torquatus*	WS	A	I	R, P	L, M	3
Grey fantail	*Rhipidura fuliginosa*	WS	A	I	R, P, UP, UB	S, M, L	27
Grey shrike-thrush*	*Colluricincla harmonica*	WS	A	I	P	L	1
House sparrow (introduced)	*Passer domesticus*	WG	H	G	UB	M, L	4

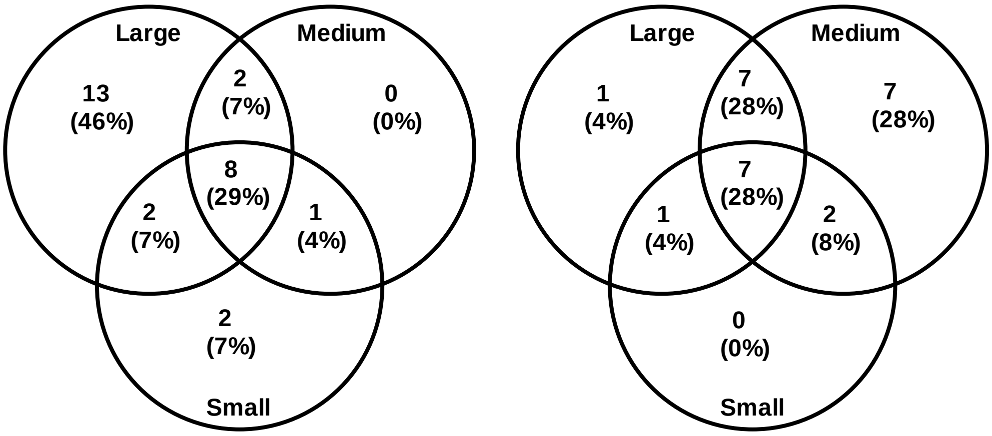
Jacky winter	*Microeca fascinans*	WS	U	I	R	S	2
Laughing kookaburra*	*Dacelo novaeguineae*	WS	H	I & Vertebrate (V)	UP	L	2
Little corella*	*Cacatua sanguinea*	WG	H	G	UP	L	5
Magpie-lark	*Grallina cyanoleuca*	WG	A	I	R, P, UP, UB	M, L	32
Mistletoebird*	*Dicaeum hirundinaceum*	WS	A	N	R, P, UP	L	3
Noisy friarbird	*Philemon corniculatus*	WS	A	N	P, UP, UB	S, M, L	26
Noisy miner	*Manorina melanocephala*	WS	A	I	R, P, UP, UB	S, M, L	59
Olive-backed oriole*	*Oriolus sagittatus*	WS	A	I	P	L	1
Pied currawong	*Strepera graculina*	WS	A	I	R, P, UP, UB	S, M, L	60
Red wattlebird	*Anthochaera carunculata*	WS	A	N	R, P, UP, UB	S, M, L	90
Red-browed finch	*Neochmia temporalis*	WS	U	G	P	M	2
Red-rumped parrot	*Psephotus haematonotus*	WS	H	G	R, P, UP, UB	M, L	23
Rufous whistler	*Pachycephala*	WS	A	I	R, P, UP,	M, L	4

	rufiventris						
Satin flycatcher*	*Myriagra cyanoleuca*	WS	A	I	P	L	2
Scarlet robin*	*Petroica multicolour*	WS	U	I	P	L	1
Silvereye	*Zosterops lateralis*	WS	A	I	R, UP	S, M, L	29
Speckled warbler	*Chthonicola sagittata*	WS	Ground (G)	I	UB	M	1
Spotted pardalote	*Pardalotus punctatus*	WS	H	I	R, UP, UB	S, M, L	20
Striated pardalote	*Pardalotus striatus*	WS	H	I	R, P, UP, UB	S, M, L	63
Sulphur-crested cockatoo	*Cacatua galerita*	WG	H	G	P, UP, UB	M, L	13
Superb fairy-wren	*Malurus cyaneus*	WS	U	I	P	M	5
Superb parrot*	*Polytelis swainsonii*	WS	H	G	UP	L	5
Tree martin	*Hirundo nigricans*	WS	A	I	P	M	1
Weebill	*Smicrornis brevirostris*	WS	A	I	R, P, UP, UB	S, M, L	31
Welcome swallow*	*Hirundo neoxena*	WG	A	I	UP	L	1

Western gerygone*	*Gerygone fusca*	WS	A	I	P	L	1
White-naped honeyeater*	*Melithreptus lunatus*	WS	A	N	P	L	3
White-plumed honeyeater	*Lichenostomus penicillatus*	WS	A	N	R, P	M, L	17
White-throated gerygone*	*Gerygone olivacea*	WS	A	I	R	L	2
Willie wagtail	*Rhipidura leucophrys*	WG	A	I	R, P	M, L	8
Yellow thornbill*	*Acanthiza nana*	WS	U	I	P	L	3
Yellow-faced honeyeater	*Lichenostomus chysops*	WS	U	N	R, P, UP, UB	S, M, L	55
Yellow-rumped thornbill	*Acanthiza chrysorrhoa*	WG	A	I	R, P, UP, UB	M, L	20


(a) Reserve

(b) Pasture


(c) Urban parkland

(d) Urban built-up

Figure A1. Venn diagrams showing the number and percentage of unique (non-overlapping) and shared (overlapping) bird species at trees of different sizes (small (20-50 cm DBH; 0.05-0.19m^2 basal area); medium (51-80 cm; 0.20-0.49 m^2); and large (> 80 cm; 0.50-2.30 m^2)) located in different landscape contexts (reserves, pasture, urban parklands and urban built-up areas). The sum of values in each complete circle corresponds to the total number or total percentage of bird species contributed by sample trees (n = 6) belonging to each size category. The sum of values in all three circles corresponds to the total number or total percentage of bird species recorded at all samples trees in each landscape context (n = 18).

Table A4. Summary of generalised linear regression model (GLM) results testing the relationship between basal area (m^2) and the number of individual birds (abundance) and bird species (richness) recorded at trees located in different landscape contexts. Reserves were held as the reference level for landscape context comparisons.

Response	Term	Estimate	Standard error	*t*-value	*p*-value	McFadden's pseudo-R^2 (deviance explained)
Abundance						0.540 (full model)
	Intercept	1.442	0.271	5.235	<0.001	
	Basal area	1.098	0.137	8.027	<0.001	0.466
	Pasture	0.771	0.305	2.524	0.01	
	Urban parkland	0.766	0.303	2.526	0.01	
	Urban built-up	0.813	0.307	2.646	0.01	
Richness						0.382 (full model)
	Intercept	0.780	0.188	4.153	<0.001	
	Basal area	0.761	0.122	6.220	<0.001	0.336
	Pasture	0.462	0.221	2.092	0.04	
	Urban parkland	0.313	0.226	1.388	0.16	
	Urban built-up	0.387	0.226	1.715	0.09	

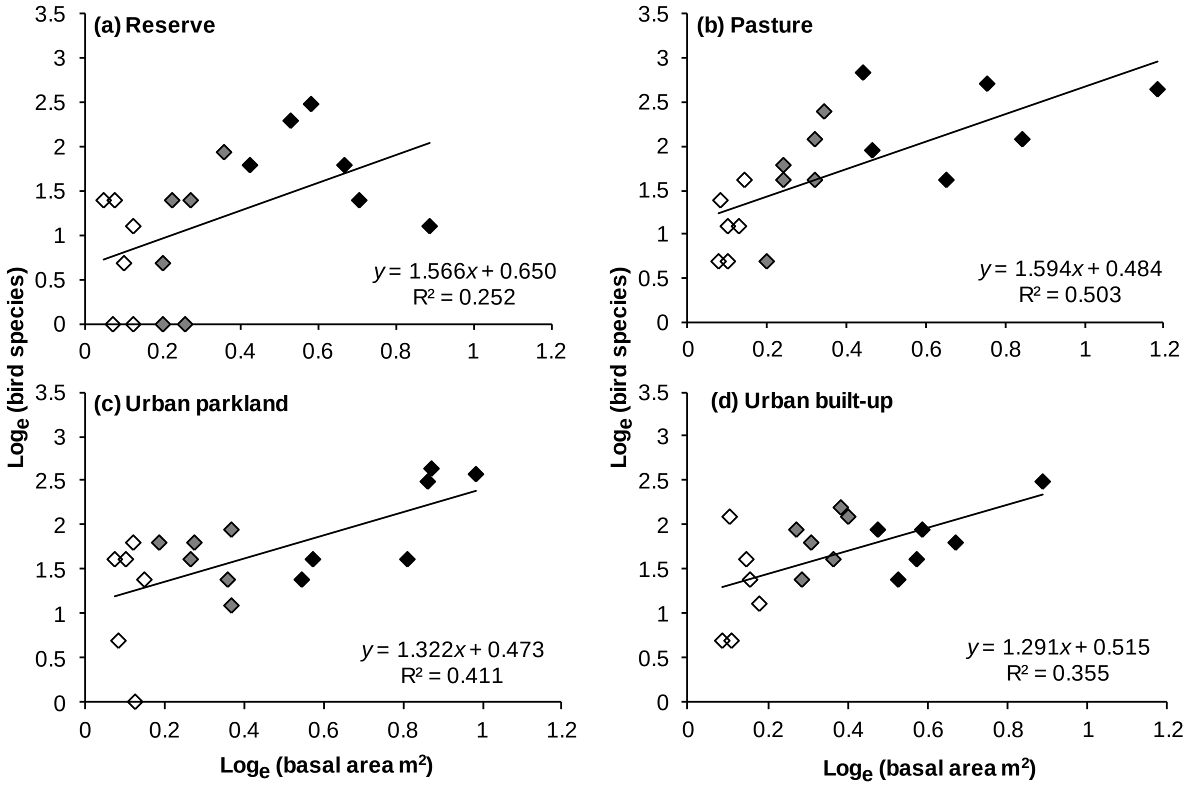


Figure A2. Plotted log-log relationships between tree basal area (m^2) and bird species in different landscape contexts. Linear forms of the species-area curve (S = CA^z) are displayed with associated R^2 correlations [i.e. log$_e$ (x + 1) transformed axes]. In all landscape contexts, an increasing trend in species number is observed with associated increases in tree size (basal area). Trees of different sizes are represented by different markers, including small trees (20-50 cm DBH; 0.05-0.19 m^2 basal area; open markers), medium trees (51-80 cm; 0.20-0.49 m^2; solid grey markers) and large trees (> 80 cm; 0.50-2.30 m^2; solid black markers).

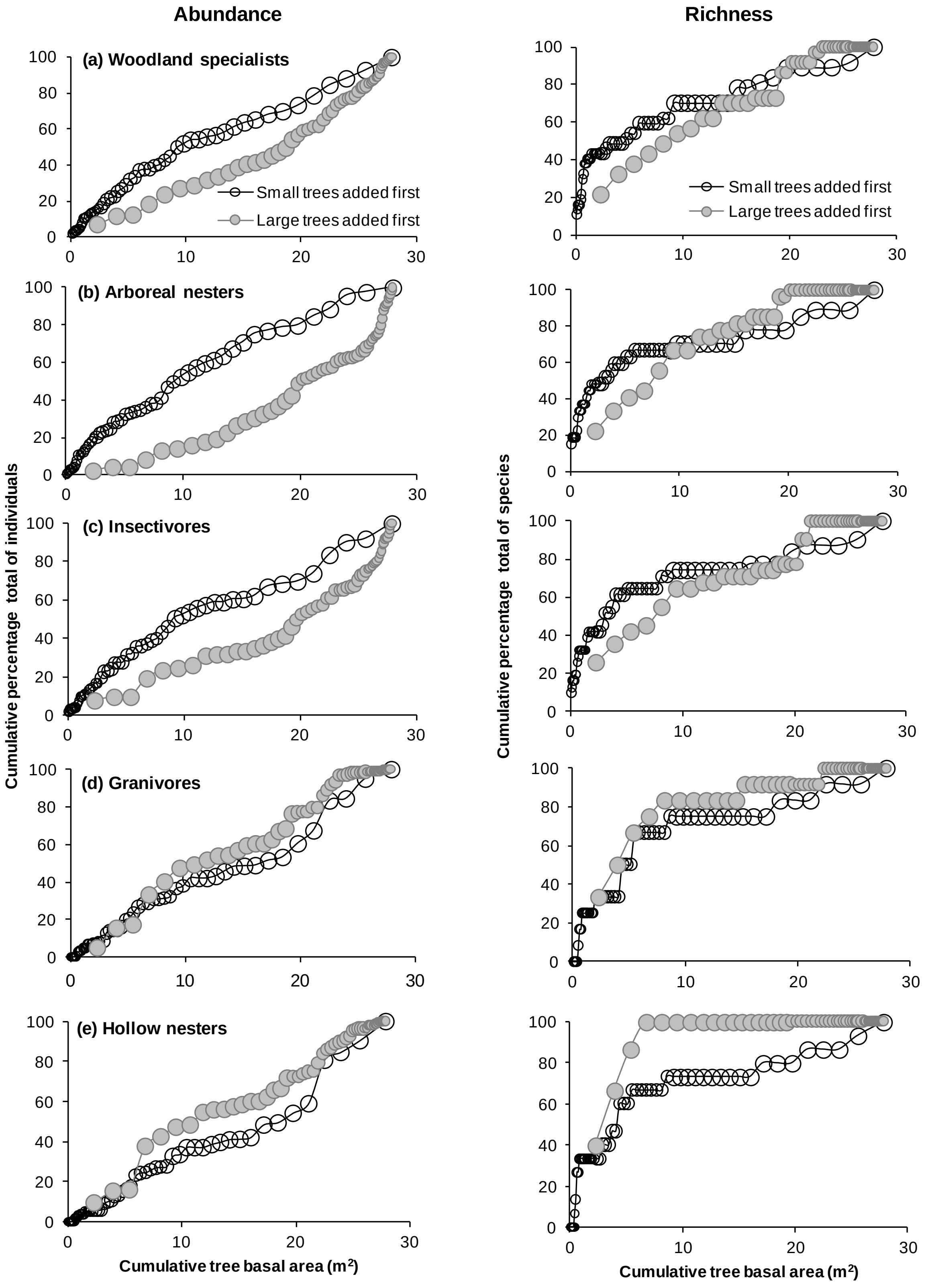


Figure A3. Cumulative percentage total of individual birds and bird species plotted against the cumulative tree basal area for five different functional bird guilds, including: woodland specialist (a), arboreal nesters (b), insectivores (c), granivores (d) and hollow nesters (e). Plotted data represents the sequential addition of small trees first and then the addition of large trees first. For each data series, different marker sizes represent trees assigned to three pre-defined tree size categories: small (20-50 cm DBH; 0.05-0.19 m^2 basal area; smallest markers); medium (51-80 cm; 0.20-0.49 m^2; medium sized markers); and large (> 80 cm; 0.50-2.30 m^2; largest markers).

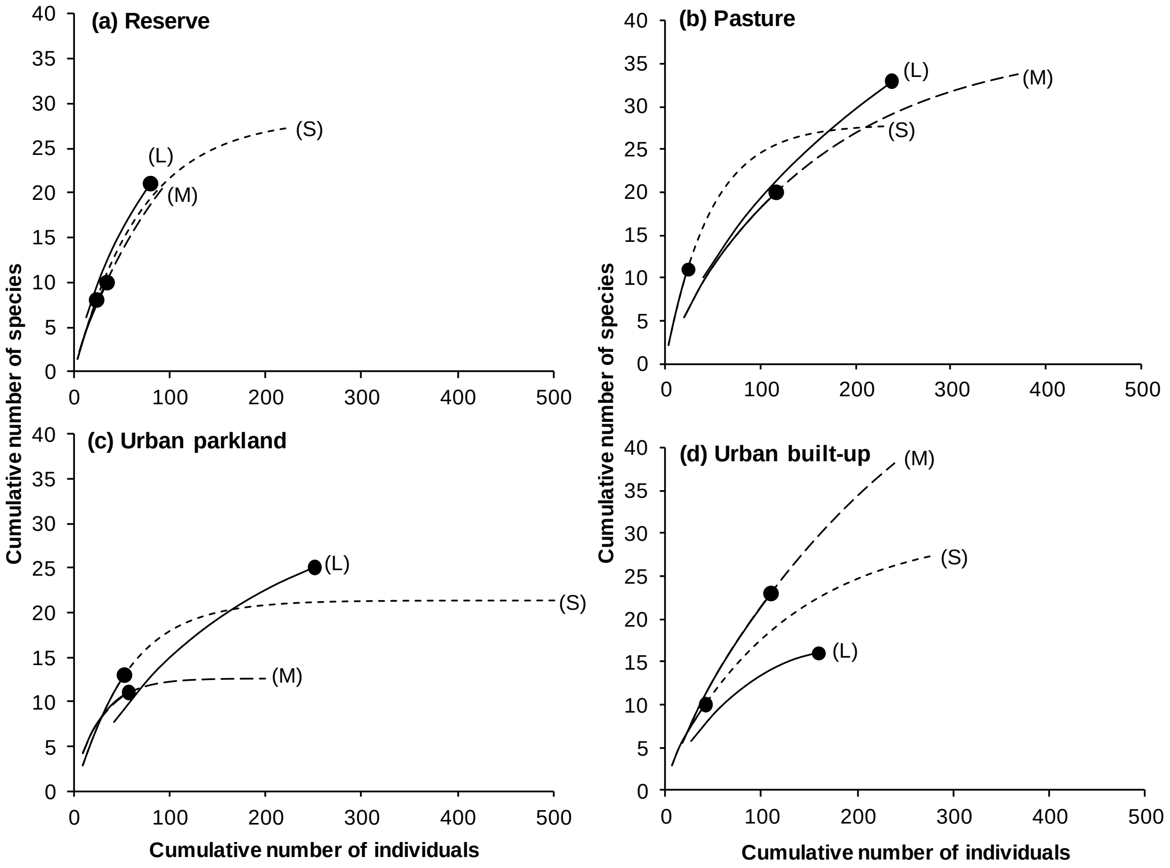


Figure A4. Individual-based rarefaction curves for birds at trees of different sizes (small trees (20-50 cm DBH; 0.05-0.19 m^2 basal area; (S)), medium trees (51-80 cm; 0.20-0.49 m^2; (M)) and large trees (> 80 cm; 0.50-2.30 m^2; (L)) located in different landscape contexts, including: reserves (a), 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 individuals. Extrapolated species accumulation curves (broken lines) represent the addition of more small and medium sample trees to achieve the equivalent cumulative basal area of large sample trees in each landscape context. Each solid marker denotes values derived from actual sample sizes (n = 6).

Table A5. Summary of rarefaction analyses for birds. The total number of individuals and species are provided for observations at trees of different sizes (small (20-50 cm DBH; 0.05-0.19 m^2 basal area); medium (51-80 cm; 0.20-0.49 m^2); and large (> 80 cm; 0.50-2.30 m^2)) located in different landscape contexts (reserves, pasture, urban parklands and urban built-up areas). Rarefaction estimators provide approximations of true species richness based on different analytical considerations (see Colwell *et al.*, 2004 and Colwell 2013 in main reference list). The expected number of accumulated individuals and species are also provided based on adding more medium and small tree samples to achieve the equivalent cumulative basal area of large sample trees in each landscape context. Mean values are presented with ± 1 standard deviation.

Design factors		Observations			Accumulated species estimators						Extrapolation		
Landscape context	Tree size	Basal area (m^2)	Total number individuals	Total number species	ACE	Chao 1	Chao 2	Jack 1	Jack 2	Boot-strap	Added samples (total)	Expected individuals	Expected species
Reserve (R)	Small (S)	0.09 ± 0.03	23 (3.8/tree)	8 (1.5/tree)	9.2	8.2 ± 0.7	16.7 ± 8.9	13.8 ± 2.0	17.9	10.4	52 (58)	222	27
R	Medium (M)	0.3 ± 0.08	34 (5.7/tree)	10 (2.2/tree)	14.0	11.2 ± 1.8	21.7 ± 11.1	16.7 ± 3.1	21.5	12.8	11 (17)	96	21
R	Large (L)	0.9 ± 0.3	80 (13.3/tree)	21 (5.8/tree)	22.2	21.4 ± 0.8	34.0 ± 9.8	31.8 ± 4.7	38.4	25.7	0 (6)	80	21
Pasture (P)	S	0.1 ± 0.03	24 (4.0/tree)	11 (2.2/tree)	18.5	18.2 ± 7.8	21.0 ± 9.1	18.5 ± 2.8	23.4	14.2	52 (58)	232	28
P	M	0.3 ± 0.07	117 (19.5/tree)	20 (5.2/tree)	23.4	21.9 ± 2.6	33.0 ± 9.8	30.8 ± 4.7	37.4	24.7	13 (19)	371	32
P	L	1.1 ± 0.6	238 (39.6/tree)	33 (9.8/tree)	39.8	38.9 ± 5.4	55.6 ± 13.9	49.7 ± 5.7	59.8	40.3	0 (6)	238	33
Urban parkland (UP)	S	0.1 ± 0.03	52 (8.6/tree)	13 (2.8/tree)	15.1	13.7 ± 1.4	19.0 ± 5.5	20.5 ± 3.1	24.4	16.4	54 (60)	520	21
UP	M	0.3 ± 0.1	57 (9.5/tree)	11 (4.1/tree)	12.0	11.3 ± 0.9	12.0 ± 1.6	14.3 ± 2.5	14.9	12.7	15 (21)	200	13
UP	L	1.2	251	25	25.7	25.2	31.1	35.0	38.7	29.7	0 (6)	251	25

		± 0.4	(41.8/tree)	(7.8/tree)		± 0.5	± 4.8	± 2.9					
Urban built-up (UB)	S	0.1 ± 0.04	42 (7/tree)	10 (2.8/tree)	14.0	11.2 ± 1.8	18.8 ± 8.9	15.8 ± 4.0	19.9	12.4	34 (40)	280	27
UB	M	0.4 ± 0.07	110 (18.3/tree)	23 (5.5/tree)	28.6	27.1 ± 4.3	51.3 ± 19.5	37.2 ± 2.4	46.9	28.9	7 (13)	238	38
UB	L	0.9 ± 0.3	160 (26.6/tree)	16 (5.8/tree)	16.4	16.1 ± 0.2	16.9 ± 1.4	20.2 ± 1.5	19.2	18.4	0 (6)	160	16

Paper V: Enriching small trees with artificial nest boxes cannot mimic the value of large trees for hollow-nesting birds

In Paper IV, I demonstrated that for some bird species and in certain landscape contexts many smaller trees could provide compensatory habitat equivalent to that of a single large tree. However, this was not a valid biodiversity offset strategy for all bird species and in some landscape contexts. In Paper V, I tested whether structurally enriching trees with artificial nest boxes can attract hollow-nesting birds.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Bistricer, G., Manning, A.D. & Gibbons, P. (2015). Enriching small trees with artificial nest boxes cannot mimic the value of large trees for hollow-nesting birds. *Restoration Ecology*, 24(2), 252-258.

Abstract

Large trees support unique habitat structures (e.g. hollows) that form over centuries and cannot be provided by small trees. Large trees are also declining in human-modified landscapes worldwide. One restoration strategy gaining popularity involves adding nest boxes to smaller trees to replicate natural hollows. However, limited empirical research has tested how hollow-nesting fauna respond to the presence of nest boxes. We asked: can the addition of nest boxes increase tree visitation by hollow-nesting birds? We conducted a before-after control-impact (BACI) experiment using 144 nest boxes and 96 sample trees comprised of three sizes (small (20-50 cm DBH), medium (51-80 cm), large (> 80 cm)) and located in four landscape contexts (reserves, pasture, urban parklands, urban built-up areas). We recorded a significant increase in hollow-nesting bird abundance and richness at large trees after nest box additions. However, the same response was not observed at medium, small or control trees. We also recorded non-significant increases in hollow-nesting bird abundance and richness at trees in modified landscapes after nest box additions compared to trees in reserves and control trees. Our results suggest that adding nest boxes to smaller sized trees may not attract hollow-nesting birds. Therefore, nest box management strategies may require re-evaluation as it is often assumed that hollow supplementation will attract hollow-using fauna and sufficiently ameliorate the loss of large, hollow-bearing trees. We advocate that large tree retention remains crucial and should be prioritized. Large trees could be effective target structures for habitat restoration, especially in modified landscapes.

Keywords: BACI, habitat supplementation, hollow-bearing trees, modified landscapes, tree cavities, tree management

Introduction

Large old trees support unique physical profiles (e.g. large complex canopies) and habitat structures (e.g. hollows, woody debris) that only form over centuries and cannot be provided by small young trees (Lindenmayer et al. 1991; Gibbons & Lindenmayer 2002; Fischer et al. 2010; Cockle et al. 2011; Stagoll et al. 2012). In human-modified landscapes (e.g. agricultural and urban landscapes), large old trees are declining due to anthropogenic pressures such as land clearance and managed tree removal (Gibbons et al. 2008; Le Roux et al. 2014a; Plieninger et al. 2015). Therefore, strategies that focus on long-term tree management are urgently needed in human-impacted environments worldwide (Vesk et al. 2008; Lindenmayer et al. 2013; Le Roux et al. 2015). This is crucial for conserving resources like hollows, which provide vital nesting opportunities for biota and can limit fauna populations (Newton 1994; Cockle et al. 2010; Manning et al. 2012).

Nest boxes bypass the extensive time periods required for hollows to form naturally as trees age and senesce (Lindenmayer et al. 2009; Goldingay et al. 2015). As a result, hollow supplementation involving the addition of nest boxes is a restoration strategy that is gaining popularity in modified landscapes, especially where large old trees and natural hollows are otherwise reduced (e.g. urban and agriculutral landscapes; Harper et al. 2005; Flaquer et al. 2006). As an example, biodiversity offset schemes sometimes seek to compensate for the loss of established hollow-bearing trees removed during development (e.g. road and housing construction) by adding nest boxes to smaller immature trees as replacement habitat for hollow-using fauna (Thomson 2006; Gibbons & Lindenmayer 2007; Roads and Traffic Authority 2011). There are some limitations with this management approach when considering animal occupancy (e.g. high rates of nest box attrition and limited occupancy by threatened taxa; Lindenmayer et al. 2009; but see also Goldingay et al. 2015). Occupancy outcomes tend to be the primary focus of nest box studies, but a complementary, yet relatively neglected area of research involves investigating the local responses of hollow-nesting fauna to nest box addition (Beyer & Goldingay 2006; Goldingay & Stevens 2009). As an example, the abundance of flying squirrels (*Glaucomys sabrinus*) did not increase after nest box supplementation in deciduous forests in Canada (Priol et al. 2014). In contrast, nest box supplementation in agricultural landscapes in Switzerland facilitated increased survival, fecundity and immigration in a hoopoe (*Upupa epops*) population (Berthier et al. 2012).

In this study, we asked: can the addition of nest boxes increase tree visitation by hollow-nesting birds as measured by changes in abundance and species richness at individual trees? We hypothesised that tree visitation by hollow-nesting birds would increase if nest boxes were added to: (1) small and medium trees, which support fewer natural hollows (an average of ≤ 1 hollow / tree), but not at large trees, which support more natural hollows (≥ 3 hollows / tree); and (2) trees in modified landscape contexts (pasture, urban parklands and urban built-up areas), which support fewer hollow-bearing trees (an average of ≤ 6 hollow-bearing trees / ha), but not trees in a semi-natural landscape context (reserves), which support more hollow-bearing trees (≥ 12 hollow-bearing trees / ha) (Le Roux et al. 2014b). To test our hypotheses, we conducted a before-after control-impact (BACI) nest box addition experiment. Our study provides a timely platform to discuss how habitat supplementation could be used as a restoration strategy to benefit biota in impacted landscapes.

Methods

Study area

We conducted our study in and around the city of Canberra, southeastern Australia (35°17′35.64″ S; 149°07′27.36″ E). Canberra (810 km^2) is located in a highly fragmented landscape that comprises: urban areas supporting a population of 375,000 people; agricultural land for livestock grazing; and 34 semi-natural nature reserves managed for conservation (ACT Government 2011). Native *Eucalyptus* box-gum grassy woodlands once dominated the region but land clearance for farming and urban development has led to an approximately 95% decline in box-gum grassy woodlands, which are now listed as a critically endangered ecological community (Department of the Environment 2015). As part of this decline, the loss of large, hollow-bearing trees has been identified as a key threatening process for hollow-using species (Schedule 3, *Threatened Species Conservation Act 1995*). In southeastern Australia, it is estimated that at least 17% of bird species, 42% of mammal species, and 28% of reptile species use natural hollows (Gibbons & Lindenmayer 1997).

Experimental design

We randomly selected 96 sample trees (native *Eucalyptus* spp.) of three tree sizes (small, 20-50 cm diameter at breast height (DBH)); medium, 51-80 cm DBH; and large, ≥ 80 cm DBH), which were located in four landscape contexts with varying degrees of modification (semi-natural reserves, grazed pastureland, urban parklands (≥ 2 ha), and urban built-up areas (e.g. residential housing)). Sample trees were at least 250 m apart to minimise spatial dependence and were located across nine reserves (average (± SE) tree density = 569 ha^{-1} ± 99; average distance to nearest tree = 6.8 m ± 0.9), four rural landholdings (133 ha^{-1} ± 56; 26.5 m ± 5.6), 24 urban parklands (161 ha^{-1} ± 44; 12.9 m ± 1.6) and 24 urban built-up areas (18 ha^{-1} ± 3.0; 23.9 m ± 4.1), which collectively spanned approximately 50 km^2. We installed 144 nest boxes at half of our sample trees (three nest boxes per tree), which resulted in 48 nest box trees and 48 control trees (unpaired). Therefore, we had a balanced design with four replicates by treatment group, tree size and landscape context. There was no significant difference ($p > 0.05$; Kruskal-Wallis ANOVA) between the structural habitat attributes measured at control and nest box trees, including tree height, canopy width, number of natural hollows, number of mistletoe, % dead canopy branches, % peeling bark, and within a 10 m radius: number of fallen logs, number of native shrubs, and % litter cover.

At each nest box tree, we installed three nest boxes in February 2013, each with a different entrance size (small, 20 or 35 mm; medium, 55 or 75 mm; large, 95 or 115 mm), which was equivalent to the average number and entrance sizes of naturally occurring hollows found at large *Eucalyptus* trees in our study region (Le Roux et al. 2014b). Nest boxes were installed at different heights (3, 4, 5 m) and orientations (north, south, east, west) ensuring that for each entrance size an equal number of nest boxes were secured at different heights (8 boxes / height) and orientations (6 boxes / orientation), respectively (Fig. 1). All nest boxes were of a rectangular design made from untreated hardwood (*Eucalyptus* spp.) with equal volumes (0.03 m^3) and dimensions (height 45 x width 25 x depth 25 cm).

Figure 1. Photograph of a sample tree showing the arrangement of added nest boxes.

Bird surveys

We conducted two separate fixed point visual bird surveys (20 minutes / tree) at each of our 96 sample trees in 2012 (before nest box addition) and again in 2013 (after nest box addition). Surveys involved sitting > 5 m from each tree and recording the number of individuals and species of hollow-nesting birds that came into direct contact with each tree. Surveys were undertaken in October of each year coinciding with the peak breeding period for hollow-nesting birds in southeastern Australia. Surveys were undertaken by the same observer (DSL) between dawn and 11 am, avoiding unfavourable weather. In this study, we focused only on tree-level bird responses, not on nest box occupancy outcomes, which are presented in a separate research study (Le Roux et al. 2016).

Data analyses

We used an analysis of covariance (ANCOVA) to test if the addition of nest boxes to trees had a significant effect on the number of hollow-nesting birds and species visiting sample trees. We calculated differences in abundance and richness between survey periods for each tree ($X_{\text{diff}} = \text{after}_i - \text{before}_i$). We fitted ‘treatment’ (control vs. nest box trees), ‘tree size’ (small, medium, and large) and ‘landscape context’ (reserve, pasture, urban parkland, and urban built-up areas) as crossed fixed effects. We also tested the effect of structural habitat covariates measured at each tree (see attributes listed above). No covariates were significant and all were excluded from our final ANOVA models. We were unable to test treatment effects for individual species due to small sample sizes. Native and exotic species were pooled in our analyses for a general representation of the hollow-nesting bird community.

Results

We recorded a total of 456 individual birds identified to 12 hollow-nesting species (9 native, 3 exotic; Table 1). We found a significant interaction between ‘treatment’ and ‘tree size’ for hollow-nesting bird abundance (mean squares = 43.67, degrees of freedom = 2, *p*-value = 0.037; Fig. 2a) and species richness (m.s. = 5.54, d.f. = 2, $p = 0.005$; Fig. 2b). There was a significant increase in the number of individuals (3.62 ± 1.48) and species (1.19 ± 0.38) recorded at large trees after the addition of nest boxes. However, we recorded no significant increase in the number of hollow-nesting birds and species at medium and small trees after the addition of nest boxes or at control trees.

We found no significant interaction between ‘treatment’ and ‘landscape context’ for hollow-nesting bird abundance (m.s. = 33.29, d.f. = 3, $p = 0.052$; Fig. 2c) and species richness (m.s. = 1.24, d.f. = 3, $p = 0.291$; Fig. 2d). However, we did observe an increase in the number of hollow-nesting individuals and species recorded at trees located in pasture, urban parklands and urban built-up areas (modified landscape contexts) after the addition of nest boxes compared with trees located in reserves (semi-natural landscape context) and control trees.

Table 1. Hollow-nesting bird species recorded at sample trees. A summary of corresponding means and totals showing increases (+) or decreases (-) in the number of individuals (abundance) visiting control trees (n = 48) and nest box trees (n = 48). Introduced species are marked with an asterisk.

Common name	Scientific name	Mean change / tree		Total change		Total number of individuals recorded
		Control	Nest box	Control	Nest box	
Australian king parrot	*Alisterus scapularis*	0.00	-0.19	0	-9	11
Common myna*	*Acridotheres tristis*	0.06	0.08	+3	+4	23
Common starling*	*Sturnus vulgaris*	0.04	0.44	+2	+20	83
Crimson rosella	*Platycercus elegans*	-0.54	0.16	-28	+8	88
Eastern rosella	*Platycercus eximius*	-0.10	0.33	-5	+22	129
Galah	*Cacatua roseicapilla*	0.00	0.06	0	+3	31
House sparrow*	*Passer domesticus*	-0.04	-0.04	-2	-2	4
Little corella	*Cacatua sanguinea*	-0.02	0.00	-1	0	1
Red-rumped parrot	*Psephotus haematonotus*	0.04	0.08	+2	+4	14
Spotted pardalote	*Pardalotus punctatus*	0.00	-0.02	0	-1	7
Striated pardalote	*Pardalotus striatus*	0.08	0.15	+4	+7	47
Sulphur-crested cockatoo	*Cacatua galerita*	0.00	-0.08	0	-4	18

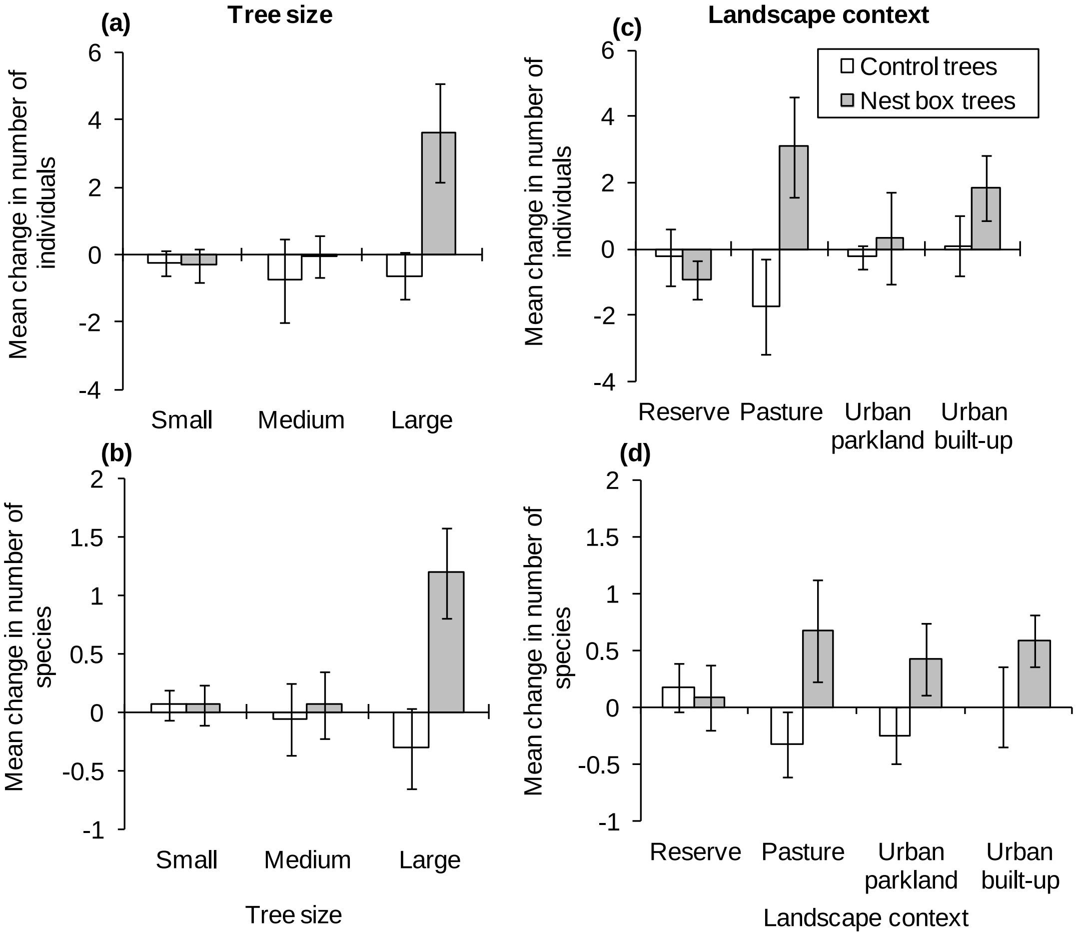


Figure 2. Mean change (± SE) in the number of individuals (abundance) and species (richness) of hollow-nesting birds visiting control and nest box trees of different sizes (small (20-50 cm DBH), medium (51-80 cm), large (>80 cm); panels a and b) located in landscape contexts with varying degrees of modification (reserves, pasture, urban parklands, urban built-up areas; panels c and d).

Discussion

To date, only limited research has been undertaken to empirically test how habitat supplementation efforts affect wildlife responses at local and landscape scales (von Post & Smith 2015). In our study, we found a significant increase in the number of individuals and species of hollow-nesting birds that visited large trees after the addition of nest boxes (Fig. 2). However, the same trend was not observed at medium and small trees after the addition of nest boxes or at control trees. This result did not support our first hypothesis, which predicted a converse response pattern given differences in the availability of natural hollows at individual trees of different sizes (Gibbons & Lindenmayer 2002). This finding highlights that simply adding nest boxes to smaller trees in an attempt to replicate the availability of natural hollows found at large trees may not be sufficient to attract hollow-nesting birds.

We found tentative support for our second hypothesis, in which we predicted an increase in hollow-nesting bird visitation only at trees located in modified landscapes where fewer hollow-bearing trees persist (Le Roux et al. 2014b). We recorded non-significant increases in the number of individuals and species of hollow-nesting birds visiting nest box trees located in pasture, urban parklands and urban built-up areas compared with nest box trees located in semi-natural reserves and at control trees (Fig. 2). This finding is congruent with other studies that have demonstrated that adding nest boxes to habitats with a high availability of natural hollows could lead to subdued responses by hollow-nesting species (Smith & Agnew 2002; Durant et al. 2009; Lindenmayer et al. 2009). Therefore, practitioners (e.g. land managers and urban developers) could preferentially add nest boxes to scattered trees located in disturbed landscapes where natural hollow availability is likely to be most reduced due to human activities, such as paddock and urban tree clearance (Gibbons et al. 2008; Le Roux et al. 2014a). Attracting hollow-nesting birds to trees in human-modified landscapes could potentially facilitate other behavioural responses such as increased hollow occupancy, breeding and dispersal (Manning et al. 2009; Berthier et al. 2012; von Post & Smith 2015).

We did not identify any significant habitat attributes (covariates) at sample trees, including the number of natural hollows, which could further explain why we observed such contrasting response patterns at trees of different sizes. These results suggest that large trees are attractive to hollow-nesting birds because they collectively support many different attributes and habitat structures (e.g. peeling bark and large canopies for perching) that smaller trees lack. Replicating other habitat structures in addition to hollows may thus be needed to attract hollow-nesting birds to smaller trees. However, some physical features of large trees are not replicable (e.g. tree height, canopy width). Our results suggest that adding nest boxes to large trees, thereby further enriching a structure already rich in resources, can make large trees even more attractive to hollow-nesting avifauna. However, enriching smaller trees with nest boxes, where many structural attributes are missing, is unlikely to encourage hollow-nesting birds to visit these trees. Therefore, nest box management strategies may require re-evaluation as it is often assumed that artificially replicating hollows at smaller trees will attract hollow-using fauna and be sufficient to ameliorate the loss of large, hollow-bearing trees. Instead, our findings re-enforce the importance of large tree retention, which should be a high conservation priority, especially in modified landscapes (Gibbons et al. 2008; DeMars et al. 2010; Stagoll et al. 2012; Hartel et al. 2013; Le Roux et al. 2015).

We recognise that there are limitations with our study. In particular, bird surveys undertaken over a longer period of time at sample trees both before and after nest box additions would have benefited our experiment and resulted in larger samples sizes allowing individual species responses to be tested more thoroughly (Wiebe 2011). It is also important to note that although our results are generalised to hollow-nesting birds (native and exotic species were pooled), individual species did not respond in uniform ways (Table 1). Even congeneric taxa such as the crimson (*Platycercus elegans*) and eastern rosella (*Platycercus eximius*), and spotted (*Pardalotus punctatus*) and striated pardalote (*Pardalotus striatus*), exhibited slightly different responses at control and nest box trees. We also found that some introduced species like the common starling (*Sturnus vulgaris*), which is known to proliferate in modified landscapes (Pell & Tidemann 1997), were attracted to nest box trees. Practitioners should be mindful that nest boxes could inadvertently attract undesirable exotic species as well as common native species (Grarock et al. 2013).

Our findings suggest that large scattered trees could be effective target structures for habitat supplementation efforts, especially in human-modified landscapes where many habitat structures are absent or reduced, or where the intentional removal of habitat is offset by providing compensatory habitat alternatives (Le Roux et al. 2014b). Replacing or replicating habitat structures at and around large scattered trees could increase structural heterogeneity and provide habitat benefits for a wide range of biota. Adding nest boxes could facilitate increased dispersal of hollow-nesting species through human-modified landscapes with large trees serving as attractive ‘stepping stones’ (Fischer & Lindenmayer 2002; Barth et al. 2015). However, nest box programs may not always be a feasible option as they can be expensive and the materials used often rapidly deteriorate (e.g. within 10 years; McKenney & Lindenmayer 1994; Lindenmayer et al. 2009). Carving out more ‘natural’ hollows at dead and large living trees or safely accelerating hollow formation by encouraging dead branch formation (e.g. injecting herbicides; Bull & Partridge 1986) could potentially provide longer term benefits for hollow-nesting fauna but these methods still require experimental research (Le Roux et al. 2014a). Replacing or replicating other habitat structures provided by large trees could also benefit fauna. For example, adding coarse woody debris, even as fence post piles, has been shown to increase local abundance and richness of reptiles and invertebrates (Barton et al. 2011; Shoo et al. 2014). Artificial peeling bark also has been successfully used to encourage roosting by insectivorous bats (Brandenburg 2013; Mering & Chambers 2014).

Habitat supplementation has potential as an innovative restoration strategy that warrants further research attention. This is important in human-modified landscapes worldwide (e.g. agricultural land, production forests and urban greenspace) where tens of millions of hectares of remnant vegetation have been cleared for human purposes, resulting in the loss and diminishment of habitat resources for biota (Hobbs & Norton 1996; Tilman et al. 2011; Menz et al. 2013). We encourage a re-think of traditional land and tree management regimes that often facilitate the intentional removal or ‘tidy up’ of habitat structures (e.g. clearing woody debris and pruning away dead branches; Carpaneto et al. 2010; Le Roux et al. 2014b). Innovative landscaping alternatives that seek to retain and replace habitat structures may be more ecologically sustainable and cost-effective over the long term, while also providing important benefits for wildlife (Le Roux et al. 2014b; Shoo et al. 2014; Garbuzov et al. 2015, Ikin et al. 2015).

In this study, we have empirically demonstrated that nest boxes could be used to increase tree visitation by hollow-nesting birds at large native trees. Our results underscore the importance of retaining large trees, which provide unique habitat structures that may be difficult to replicate at smaller trees in the short-term. We also encourage longer-term field experiments to empirically test the effectiveness of habitat supplementation tactics by quantifying changes in wildlife responses through space and time.

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Paper VI: Effects of entrance size, tree size and landscape context on nest box occupancy: considerations for management and biodiversity offsets

In Paper V, I showed that adding nest boxes to smaller sized trees may be insufficient to attract hollow-using avifauna, which depends on large, hollow-bearing trees for survival. A better understanding of which spatial factors influence animal occupancy outcomes is also important to improve applied nest box programs. In Paper VI, I investigated the effects of entrance size, tree size and landscape context on nest box occupancy by fauna.

Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Bistricer, G., Manning, A.D. & Gibbons, P. (2016). Effects of entrance size, tree size and landscape context on nest box occupancy: considerations for management and biodiversity offsets. *Forest Ecology and Management*, 366, 135-142.

Abstract

The effectiveness of nest boxes as a management and biodiversity offset tool remains equivocal and controversial. Improving nest box programs requires urgent empirical research to identify the spatial factors that affect occupancy outcomes. Understanding which fine, local and landscape-level attributes influence nest box selection by wildlife can assist practitioners in refining nest box designs and placement in the field. We asked: Does entrance size, tree size and landscape context affect nest box occupancy? We monitored 144 nest boxes with six different entrance sizes (20, 35, 55, 75, 95 and 115 mm diameter), secured to individual trees of three sizes (small 20-50 cm DBH, medium 51-80 cm and large > 80 cm) situated in four different landscape contexts with varying degrees of modification (reserves, pasture, urban parklands and urban built-up areas). We found that six common native and exotic species accounted for 89% of nest box occupancies. Entrance size had a significant effect on overall occupancy. Nest boxes with larger entrance sizes (115, 95, 75 and 55 mm) were occupied more (≥ 77% of nest boxes occupied) than nest boxes with smaller entrance sizes (35 and 20 mm; ≤ 45% of nest boxes occupied). Tree size and landscape context had no significant effect on overall occupancy. However, multinomial analysis revealed that entrance size and landscape context affected occupancy by common fauna (i.e. species that occupied ≥ 5% of nest boxes). Nest boxes with small (20 and 35 mm), intermediate (55 and 75 mm) and large (95 and 115 mm) entrance sizes were predominately occupied by the European honey bee *Apis mellifera*, common exotic (e.g. common myna *Acridotheres tristis*) and native birds (e.g. eastern rosella *Platycercus eximius*), and the common brushtail possum *Trichosurus vulpecula*, respectively. Nest boxes in reserves and pasture had near equal occupancy by common fauna while nest boxes in urban parklands and urban built-up areas were predominately occupied by the common brushtail possum and the European honey bee. Establishing nest boxes with different entrance sizes could maximise occupancy by a variety of common hollow-nesting species. Targeting occupancy by some species requires consideration of landscape context but not tree size. Nest boxes were predominately occupied by a few common native and exotic species, suggesting that nest boxes may not be highly effective management and biodiversity offset tools for rare and threatened

taxa in modified landscapes. Management policies and practices aimed at avoiding the loss of large, hollow-bearing trees must be prioritised.

Key words: common fauna, human-modified landscapes, large old trees, tree cavities, tree hollows, wildlife conservation

Introduction

Tree hollows (or cavities) are a critical habitat resource for fauna globally (Gibbons and Lindenmayer, 2002; Cockle *et al.*, 2011). Hollows provide shelter and breeding opportunities for mammals (Lindenmayer *et al.*, 1990), birds (Newton, 1994), reptiles (Webb and Shine, 1997), and invertebrates (Ranius, 2002). In modified landscapes worldwide (e.g. agricultural land, production forests and urban environments), human activities, such as land clearance, logging and managed tree removal, have facilitated the decline of large, hollow-bearing trees (Gibbons *et al.*, 2010; Lindenmayer *et al.*, 2012; Le Roux *et al.*, 2014a; McIntyre *et al.*, 2015). Reduced availability of hollow-bearing trees can have serious conservation implications for hollow-using fauna, especially for obligate hollow-nesters that may face population bottlenecks and extinction (Cockle *et al.*, 2010; Manning *et al.*, 2012). Time lags associated with hollow formation mean that some management strategies aimed at arresting hollow decline (e.g. increasing tree recruitment) will be unable to alleviate short-term deficits in hollow availability (Gibbons *et al.*, 2008; Manning *et al.*, 2012; Le Roux *et al.*, 2014a). Nest boxes offer an alternative management strategy that bypasses the time needed for hollows to form naturally, potentially providing immediate benefits for hollow-using species (Lindenmayer *et al.*, 2009; Berthier *et al.*, 2012).

In some cases, the recovery of hollow-nesting animal populations has partly been attributed to nest box additions (e.g. southern flying squirrels *Glaucomys volans* in logged plantations; Taulman *et al.*, 1998; see also Goldingay *et al.*, 2015). However, in many other cases, the efficacy of nest box programs remains questionable and controversial because of low occupancy rates and exploitation by non-target fauna (Grarock *et al.*, 2013; Priol *et al.*, 2014). A further limitation of nest box programs is the rapid rate of nest box attrition due to damage and decay of materials. Lindenmayer *et al.* (2009) found that most nest boxes had decayed and fallen from trees within ten years limiting long-term effectiveness for the critically endangered Leadbeater's possum *Gymnobelideus leadbeateri*. In contrast, natural hollows likely persist over much longer time periods (Gibbons *et al.*, 2000; Ranius *et al.*, 2009). A further limitation for practitioners is the high financial costs that may be associated with nest box construction, monitoring and maintenance (McKenney and Lindenmayer, 1994). These studies highlight that nest box programs supplementing natural hollows over large areas, long time periods, and for threatened species, can be exceptionally challenging to implement.

Despite the limitations outlined above, nest boxes are increasingly being employed as an engineering 'solution' to compensate for the loss of large, hollow-bearing trees removed due to human activities (e.g. Goldingay and Stevens, 2009; Roads and Traffic Authority, 2011; Peste *et al.*, 2015). However, before nest boxes can be used effectively as a management and biodiversity offset tool, it is imperative to first identify ways of improving nest box design and placement in the field. Goldingay *et al.* (2015) recently highlighted that refinements to nest box design could limit nest box use by pest fauna and improve nest box occupancy by some threatened species. Previous research studies, predominately undertaken in Europe and North America, have found that nest box selection by fauna (mostly birds) can be affected in complex ways by a variety of fine, local, and landscape level attributes (e.g. Herlugson, 1981; Finch, 1989; Blem and Blem, 1991; Bortolotti, 1994; Bolton *et al.*, 2004; Ardia *et al.*, 2006; Smith *et al.*, 2007; Lambrechts *et al.*, 2010; Björklund *et al.*, 2013). By comparison, only a few Australian studies have empirically tested whether species show a preference for specific nest box designs and placement (e.g. Menkhorst, 1984; Smith and Agnew, 2002; Harper *et al.*, 2005; Goldingay *et al.*, 2007; Durant *et al.*, 2009; Lindenmayer *et al.*, 2009; Goldingay *et al.*, 2015). More studies are still urgently needed to investigate nest box selection by fauna and, in doing so, also evaluate whether nest box programs can effectively achieve applied conservation objectives.

In this study, we asked: does entrance size, tree size, and landscape context affect nest box occupancy? These spatial factors were investigated because they can be relatively easily manipulated at the construction and installation phase of nest box programs to potentially influence on-the-ground occupancy outcomes. We tested five predictions (see Table 1): (1) nest boxes with larger entrance sizes will be occupied more than nest boxes with smaller entrance sizes; (2) nest boxes with larger and smaller entrance sizes will be occupied by proportionally larger and smaller-bodied animals, respectively; (3) nest boxes secured to small and medium sized trees, which support fewer natural hollows, will be occupied more than nest boxes secured to large trees, which support more natural hollows; (4) nest boxes placed in modified landscapes, which support fewer hollow-bearing trees, will be occupied more than nest boxes placed in a semi-natural landscape, which supports more hollow-bearing trees; and (5) common adaptable native and exotic species will occupy more nest boxes placed in modified landscapes than nest boxes placed in a semi-natural landscape.

Materials and methods

Study area

We conducted our study in Canberra, Australian Capital Territory (ACT), southeastern Australia. Canberra (covering an area of approximately 810 km^2) is located in a fragmented landscape comprising: urban areas supporting 375,000 people; agricultural land for livestock grazing; and 34 nature reserves managed for conservation (ACT Government, 2011). Land clearance for farming and urban development has led to an approximately 95% decline in box-gum grassy woodlands that once dominated this region and is now listed as a critically endangered ecological community (Department of the Environment, 2015). As part of this decline, the loss of large, hollow-bearing trees has been identified as a key threatening process (New South Wales Government, 1995). In southeastern Australia, it is estimated that 17% of bird, 42% of mammal, and 28% of reptile species use natural hollows (Gibbons and Lindenmayer, 1997).

Table 1. A summary of study predictions and ecological justifications underpinning these.

Factor	Prediction	Ecological justification
Entrance size	(i) Nest boxes with larger entrance sizes will be occupied more than nest boxes with smaller entrance sizes.	Small hollows tend to be naturally more abundant than large hollows and may thus be in less demand by fauna (e.g. Gibbons *et al.*, 2002; Le Roux *et al.*, 2014b). Larger hollows are also likely to be accessed by more species than smaller hollows (e.g. Gibbons and Lindenmayer, 2002).
Entrance size	(ii) Nest boxes with larger and smaller entrance sizes will be preferentially occupied by large and small-bodied animals, respectively.	Animals tend to occupy hollows with entrance sizes proportional to their body size to minimise risk of predation, reduce competition at nest sites, and because hollows are of a size that is accessible (e.g. Beyer and Goldingay, 2006; Goldingay and Stevens, 2009).
Tree size	(iii) Nest boxes secured to small (20-50 cm DBH) and medium sized trees (51-80 cm DBH), which support fewer natural hollows, will be occupied more than nest boxes secured to large trees (> 80 cm DBH), which support more natural hollows.	The number of hollows available at the tree can affect the likelihood of hollow occupancy (e.g. Gibbons *et al.*, 2002; Koch *et al.*, 2008).
Landscape context	(iv) Nest boxes placed in modified landscapes (pasture, urban parklands, urban built-up areas), which support fewer hollow-bearing trees, will be occupied more than nest boxes placed in a semi-natural landscape (reserve), which supports more hollow-bearing trees.	The number of hollow-bearing trees available in the landscape can affect the likelihood of hollow occupancy (e.g. Smith and Agnew, 2002; Cockle *et al.*, 2010).

Landscape context	(v) Common adaptable native and exotic species will preferentially occupy nest boxes placed in modified landscapes than nest boxes placed in a semi-natural landscape.	Common adaptable native and exotic species tend to be tolerant of human disturbance and have a high propensity to persist in modified landscapes and exploit limited resources (Lindenmayer *et al.*, 2009; Grarock *et al.*, 2013).

Experimental design

We stratified our study area into four dominant landscape contexts representing varying degrees of modification and natural hollow availability (Table 2): (1) reserves (semi-natural conservation areas); (2) pasture (grazed agricultural land); and public urban greenspace (≥ 0.2 ha) subdivided into (3) parklands and (4) roadside margins in built-up residential areas. In each landscape context, we randomly selected 12 trees on which to secure nest boxes (nest box trees). Trees were selected from within randomly allocated 20 x 50 m vegetation plots and were located across nine reserves (average (± SE) tree density (per 0.1 ha) = 56.9 ± 9.9; average distance to nearest tree (m) = 6.8 ± 0.9), four rural landholdings (13.3 ± 5.6; 26.5 ± 5.6), 12 urban parklands (16.1 ± 4.4; 12.9 ± 1.6) and 12 urban built-up areas (1.8 ± 0.3; 23.9 ± 4.1), which collectively spanned approximately 50 km^2. All nest box trees were spaced > 250 m apart to minimise spatial dependence and were restricted to native *Eucalyptus* species. Tree sizes included: 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 four replicates, resulting in 48 nest box trees. The DBH, height and canopy width of nest box trees in each tree size category did not differ significantly across landscape contexts ($p > 0.05$; Kruskal-Wallis ANOVAs).

We installed a total of 144 nest boxes. Three nest boxes were secured to each tree (using a wooden panel/backboard and galvanised hardware), which was equivalent to the average number of natural hollows observed at large trees in our study area (Table 2; Figure S1). Each nest box installed per tree had a different circular entrance size: one small (20 or 35 mm diameter); one intermediate (55 or 75 mm) and one large (95 or 115 mm), which was reflective of the entrance size variations observed for natural hollows at native trees (Table 2). We established an equal number (n = 24) of nest boxes for all six entrance sizes, replicated equally by landscape context and tree size treatments. Each nest box was installed at a different height (3, 4, 5 m) and orientation (north, south, east, west), ensuring that, for each entrance size, an equal number of nest boxes where located at different heights (8 boxes / height) and orientations (6 boxes / orientation), respectively. Nest boxes were of a standard rectangular design made from untreated plywood (mixed hardwood *Eucalyptus* spp.) with equal volumes (0.028 m^3) and dimensions (height 45 cm x width 25 cm x depth 25 cm).

Table 2. The abundance (mean ± SE) of natural hollows (≥ 20 mm) with different entrance sizes, at different tree sizes, and in different landscape contexts.

* Measurements derived using vegetation plots (50 x 20 m; 0.1 ha) conducted at 300 random locations (n = 100 plots / landscape context); ** measurements derived from detailed visual assessments conducted at 120 randomly selected sample trees (n = 30 trees / landscape context; see details described in Le Roux *et al.*, 2014b; Le Roux *et al.*, 2015a).

Factor	Natural hollow availability
Entrance size*	Hollows / ha
Small (20-50 mm)	15.83 ± 1.91
Medium (51-100 mm)	5.63 ± 0.77
Large (> 100 mm)	6.40 ± 0.92
Tree size** (Diameter at breast height, DBH)	Hollows / tree
Small (20-50 cm)	0.00 ± 0.00
Medium (51-80 cm)	1.25 ± 0.35
Large (> 80 cm)	2.97 ± 0.89
Landscape context*	Hollow-bearing trees / ha
Semi-natural reserves	12.1 ± 1.64
Grazed pasture	4.70 ± 0.74
Public urban greenspace (≥ 0.2 ha)	5.70 ± 1.08

Data collection

We inspected nest boxes to confirm animal occupancy in 2013 and 2014. We restricted inspections to late winter and early summer (August-December) to maximise detection of animals using nest boxes for breeding over this period. Therefore, we completed ten checks per nest box. Nest boxes were inspected using a wireless camera (Signet, QC8712, Australia) and extension pole (Hastings, E-50, USA), enabling non-invasive observations. ‘Occupancy’ was defined as an animal being inside a nest box at the time of inspection or conclusive evidence of current occupancy (e.g. nesting material and eggs).

Data analyses

For all analyses, we pooled data across inspections and survey years. That is, repeated observations of occupancy across inspections were treated as a single occupancy record. We excluded nest boxes (n = 4; 2.7% of nest boxes) where entrance sizes were increased by > 10 mm due to gnawing by animals, which resulted in a sample of 140 nest boxes.

1. Factors affecting overall occupancy

We used a generalised linear mixed model (logit link) to determine whether nest box occupancy was affected by entrance size, tree size and landscape context. We fitted ‘entrance size’, ‘tree size’ and ‘landscape context’ as fixed categorical effects and ‘tree identity’ as a random effect to account for variation between nest box trees as three nest boxes were installed per tree.

2. Factors affecting occupancy by common fauna

We used a multinomial logistic regression model to investigate differences in nest box occupancy by common fauna (species that occupied ≥ 5% of nest boxes; Table 3). These fauna represented different body size categories and included: the common brushtail possum *Trichosurus vulpecula* (body mass > 2000 g), common exotic birds (common myna *Acridotheres tristis* and common starling *Sturnus vulgaris*; 50-150 g), common native birds (eastern rosella *Platycercus eximius* and crimson rosella *P. elegans*; 50-150 g), and the European honey bee *Apis mellifera* (< 2 g). ‘No occupancy’ was an additional response category. We recorded seven instances where different animal species occupied the same nest box, which we excluded from this analysis resulting in a sample of 133 nest boxes. ‘Entrance size’, ‘tree size’ and ‘landscape context’ were fitted as fixed categorical effects in our starting model and we used an information-theoretic approach to select the model of best fit by ranking models based on Akaike’s Information Criterion values (AIC).

Results

We found that 69% of nest boxes (n = 99) were occupied by fauna. Twelve species occupied nest boxes, including three mammal species, eight bird species, and one invertebrate species (Table 3). Six common species accounted for 89% of occupancies (common brushtail possum, common myna, common starling, eastern rosella, crimson rosella, and the European honey bee). The sugar glider *Petaurus breviceps* and Australian owlet-nightjar *Aegotheles cristatus* rarely occupied nest boxes and only in reserves. No species that occupied nest boxes were of conservation concern. Four species were invasive pests (common myna, common starling, the European honey bee and the black rat *Rattus rattus*).

Factors affecting overall occupancy

Entrance size had a significant effect on nest box occupancy (Wald = 50.13, df = 5, *p* < 0.001; Table S1). More nest boxes with larger entrance sizes (55, 75, 95 and 115 mm) were occupied (an average of 77-96% of nest boxes occupied) than nest boxes with smaller entrance sizes (20 and 35 mm; 25-46%; Fig. 1(i)).

We found no significant effect of tree size (Wald = 0.01, df = 2, *p* = 0.99) or landscape context (Wald = 1.18, df = 3, *p* = 0.76) on nest box occupancy. A near equal number of nest boxes were occupied when secured to small (72%), medium (68%) and large trees (63%; Fig. 1(ii)) and when placed in reserves (64%), pasture (69%), urban parklands (65%) and urban built-up areas (74%; Fig. 1(iii)).

Table 3. Summary of nest box occupancy by fauna.

*R = reserve, P = pasture, UP = urban parkland, UB = Urban built-up; **S = small (20-50cm), M = medium (51-80 cm), L = large (> 80 cm).

Taxonomic group	Common name	Scientific name	Introduced / native	Landscape Context*	Tree size (DBH)**	Nest box entrance size (mm)	Number of nest boxes occupied
Mammal	Black rat	*Rattus rattus*	Introduced	R, UP, UB	S, M, L	35, 55, 75, 115	5 (3.47%)
Mammal	Common brushtail possum	*Trichosurus vulpecula*	Native	R, P, UP, UB	S, M, L	75, 95, 115	42 (29.16%)
Mammal	Sugar glider	*Petaurus breviceps*	Native	R	S, M	75, 95	2 (1.38%)
Bird	Australian owlet-nightjar	*Aegotheles cristatus*	Native	R	M, L	55, 115	3 (2.08%)
Bird	Australian wood-duck	*Chenonetta jubata*	Native	P, UB	M, L	115	2 (1.38%)
Bird	Common myna	*Acridotheres tristis*	Introduced	R, UP, UB	S, M	55, 75, 95, 115	9 (7.85%)
Bird	Common starling	*Sturnus vulgaris*	Introduced	R, P	S, M, L	55	6 (4.26%)
Bird	Crimson rosella	*Platycercus elegans*	Native	R, P, UP	S, M, L	75, 115	6 (4.26%)
Bird	Eastern rosella	*Platycercus eximius*	Native	R, P, UP	S, M, L	55, 75, 95	7 (4.86%)
Bird	Galah	*Eolophus roseicapilla*	Native	P	M	95	1 (0.69%)
Bird	Sulphur-crested cockatoo	*Cacatua galerita*	Native	P, UP	S, L	75, 115	2 (1.38%)
Invertebrate	European honey bee	*Apis mellifera*	Introduced	R, P, UP, UB	S, M, L	20, 35, 55	18 (12.50%)
Total: occupied							99 (68.75%)
Total: unoccupied							45 (31.25%)
Grand total							144

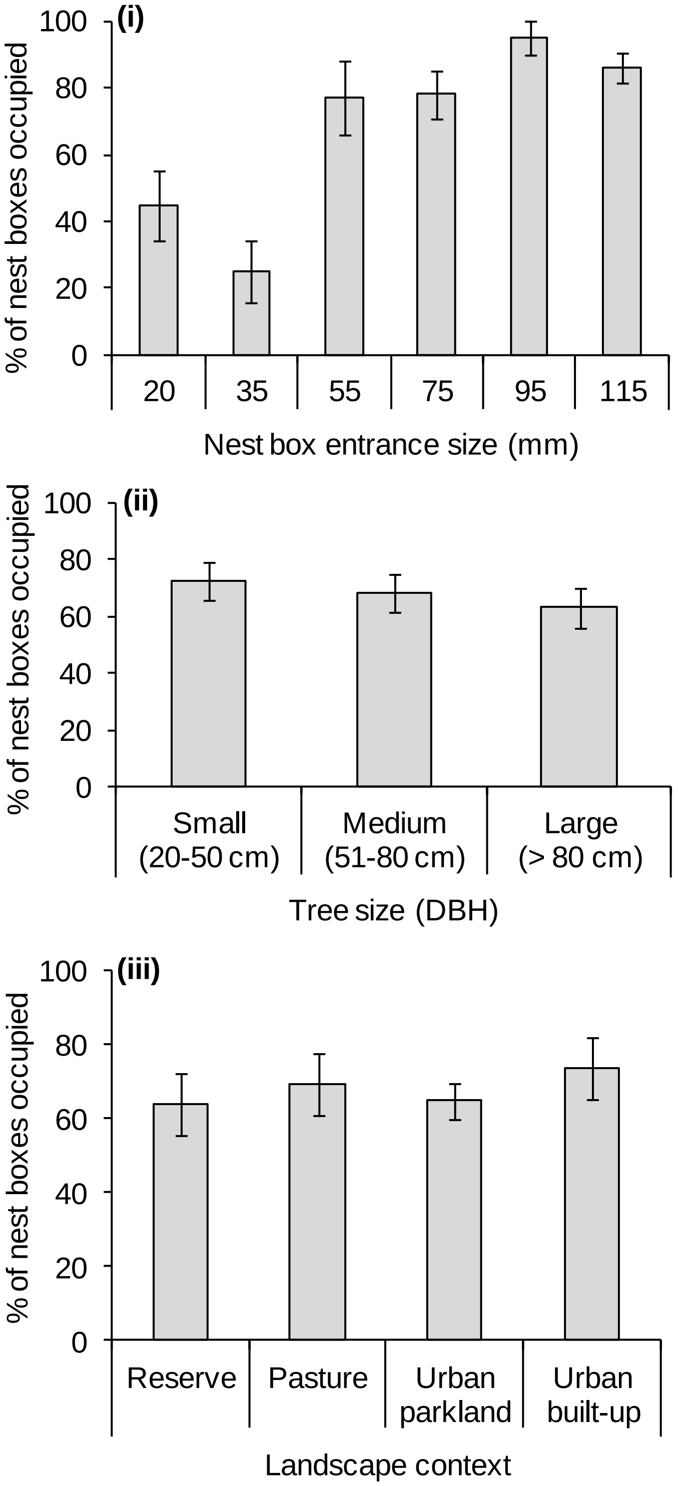

Figure 1. Percentage (mean ± SE) of nest boxes (n = 140) occupied: (i) with different entrance sizes (20, 35, 55, 75, 95, 115 mm); (ii) when secured to trees of different sizes (small, 20-50 cm DBH; medium, 51-80 cm; large, > 80 cm); and (iii) when placed in landscape contexts with varying degrees of modification (reserves, pasture, urban parklands, urban built-up areas).

Factors affecting occupancy by common fauna

Our best supported multinomial model predicting occupancy by common fauna (species that occupied ≥ 5% of nest boxes) contained two factors: nest box entrance size and landscape context (Table S2-S4).

Common fauna occupied nest boxes with entrance sizes proportional to their body size. Nest boxes with an entrance of 20 and 35 mm were unoccupied (54% and 82%, respectively; Fig. 2(i)) or occupied by the European honey bee (< 2 g; 46%, 18%). Nest boxes with entrances of 55 and 75 mm were unoccupied (30%, 37%) or had limited occupancy by exotic birds (35%, 16%) and common native birds (50-150 g; 20%, 32%). Nest boxes with entrances of 95 and 115 mm were unoccupied (22%, 28%) or predominately occupied by the common brushtail possum (> 2000 g; 72%, 61%).

In reserves, nest boxes were unoccupied (45%), or occupied by the common brushtail possum (17%), exotic birds (17%), and the European honey bee (14%; Fig. 2(ii)). In pasture, nest boxes were unoccupied (53%) or occupied by exotic (16%) and common native birds (16%). In urban parklands, nest boxes were unoccupied (45%) or occupied by the common brushtail possum (32%). In urban built-up areas, nest boxes were unoccupied (31%) or occupied by the common brushtail possum (35%) and the European honey bee (28%).

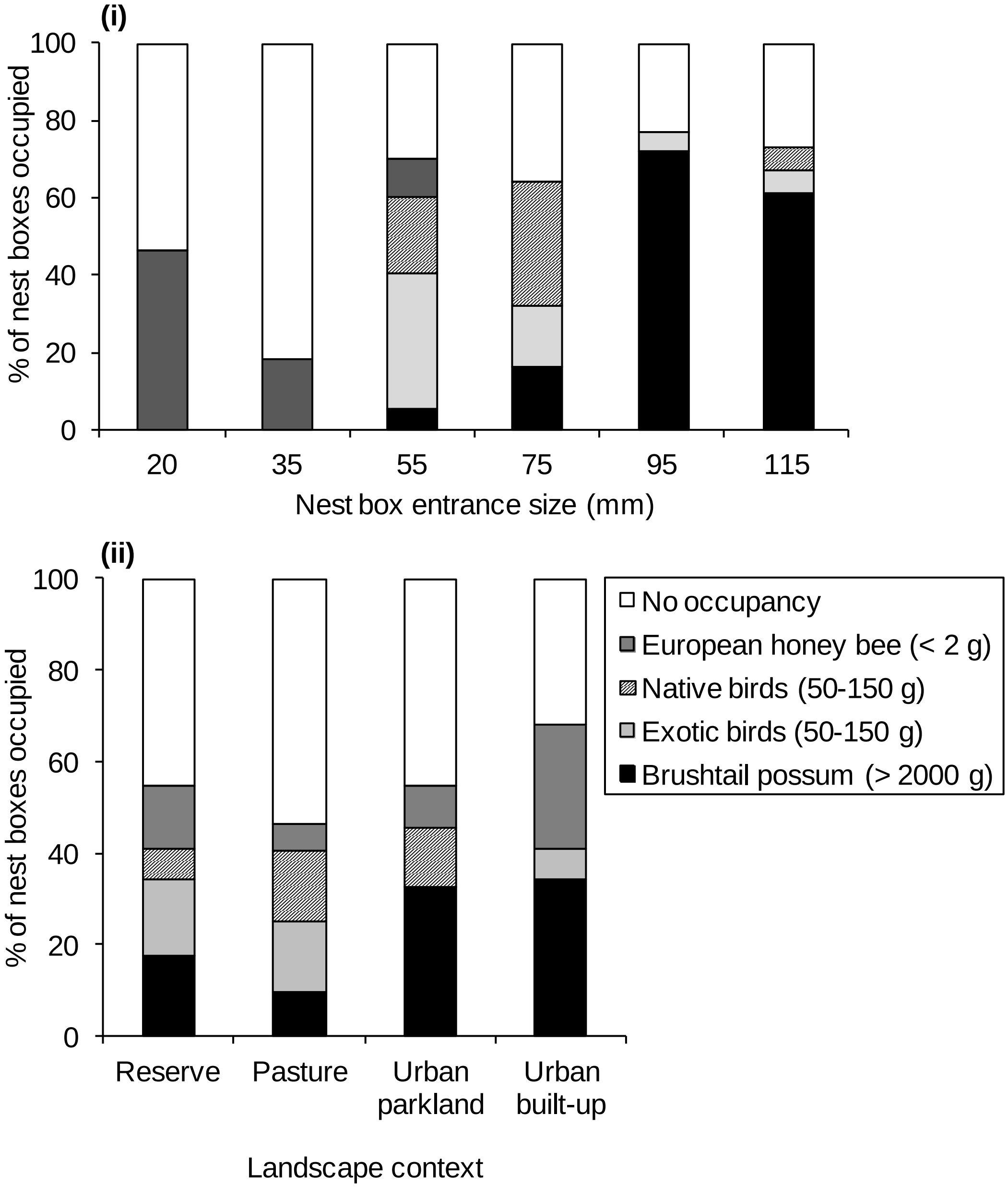

Figure 2. Percentage of nest boxes (n = 133) occupied by common fauna (species that occupied ≥ 5% of nest boxes) that: (i) had different entrance sizes (20, 35, 55, 75, 95, 115 mm); and (ii) were placed in different landscape contexts (reserves, pasture, urban parklands, urban built-up areas). Response categories included occupancy by: the common brushtail possum (> 2000 g), exotic birds (50-150 g), common native birds (50-150 g), and the European honey bee (< 2 g). 'No occupancy' was an additional response category.

Discussion

The effectiveness of nest boxes as an applied management and biodiversity offset tool remains controversial and in need of empirical research to inform on-the-ground decision-making. We conducted a nest box experiment at multiple scales to test fine, local and landscape-level effects on nest box occupancy. Entrance size had a significant effect on overall occupancy. Therefore, we advocate that practitioners should not overlook fine-scale nest box design attributes such as entrance size at the construction phase of nest box programs (see also other recent studies by Lambrechts *et al.*, 2012; Rueegger *et al.*, 2013; Goldingay *et al.*, 2015; Lindenmayer *et al.*, 2015). However, tree size and landscape context did not affect overall occupancy, suggesting that nest boxes can offer nesting opportunities to species, even when secured to smaller sized trees or when placed in disturbed environments. Common fauna occupied nest boxes in non-random ways, preferentially occupying nest boxes: (1) with entrance sizes proportional to their body size; and, for some species, (2) when located in specific landscapes contexts (urban environments). Overall, nest boxes were occupied only by a few common native and exotic species. Our findings suggests that nest boxes are unlikely to be a highly effective management and biodiversity offset tool for a multitude of hollow-dependent species, including rare and threatened taxa of highest conservation concern, particularly in landscapes characterised by increased modification. However, several case studies have highlighted the relative success of nest box programs for some threatened species in different landscape contexts (e.g. Libois *et al.*, 2012; Olah *et al.*, 2014; Goldingay *et al.*, 2015).

Spatial factors affecting occupancy

As expected, nest boxes with larger entrance sizes were occupied more than nest boxes with smaller entrance sizes. Small natural hollows (20-50 mm) can form even in relatively young trees (small and medium trees) and thus tend to be more abundant compared to large natural hollows (> 50 mm), which can take much longer to form, typically only in large old trees (Lindenmayer *et al.*, 1993; Blakely *et al.*, 2008). Therefore, small hollows may be in less demand compared to large hollows which are often a limiting resource for many hollow-using species (e.g. Newton, 1994; Manning *et al.*, 2004; Durant *et al.*, 2009; Goldingay *et al.*, 2015). Furthermore, a wide range of hollow-nesting animals (e.g. most hollow-nesting birds and arboreal mammals) may simply not be able to access nest boxes with very small entrances (Gibbons and Lindenmayer, 2002).

Although not tested in our study, other nest box design attributes can also affect occupancy, including nest box volume, placement height, orientation and types of construction materials used (Harper *et al.*, 2005; Ardia *et al.*, 2006). For example, insectivorous bats (Microchiroptera) tend to occupy nest boxes with narrow internal dimensions and slit entrances located at the base of nest boxes (Smith and Agnew, 2002; Flaquer *et al.*, 2006). This may explain why bats were not observed using nest boxes in our study. Similarly, some threatened hollow-nesting species may require custom-designed nest boxes with specific attributes that more closely mimic natural hollows selected by individuals (Bolton *et al.*, 2004; Brazill-Boast *et al.*, 2013; Goldingay *et al.*, 2015).

Common species preferentially occupied nest boxes with entrance sizes proportional to their body size. Preference for hollows with entrance sizes just large enough for an animal to access may be driven by selection pressures like predation and competition over limited nest sites. For example, Hakkarainen and Korpimäki (1996) suggested that small bodied Tengmalm's owls *Aegolius funereus* in Finland avoided using nest boxes with entrances > 115 mm due to risk of predation and competition by larger Eagle owls *Bubo bubo* and Ural owls *Strix uralensis*. In our study, it is possible that the common brushtail possum, which occupied 65% of nest boxes with large entrances (> 95 mm), precluded other species from using nest boxes with large entrance sizes (Harper *et al.*, 2005). This, in turn, may have facilitated increased conspecific competition between native and exotic birds at nest boxes with intermediate entrance sizes (Davis *et al.*, 2013).

Although we did not measure occupancy at natural hollows, we hypothesised that animals would preferentially occupy natural hollows over nest boxes where hollows were locally abundant at large trees (c.f. small and medium trees). Natural hollows tend to have a wider range of characteristics and potentially offer greater thermoregulatory benefits to species than nest boxes (McComb and Noble, 1981). However, we found that tree size had no significant effect on overall nest box occupancy. This is counter to other studies that have found that nest boxes secured to smaller sized trees were more likely to be occupied than when secured to larger trees, possibly owing to a lack of natural hollows at smaller trees (Durant *et al.*, 2009). One explanation for our result may be that not all large trees supported a high number of natural hollows or hollows that were suitable for occupancy (Gibbons *et al.*, 2002). For example, in urban environments, large trees may support few hollows due to tree management practices that remove dead and hollow-bearing branches for public safety (Carpaneto *et al.*, 2010; Le Roux *et al.*, 2014b). Studies on natural hollows have found that animal occupancy was more likely at trees that supported many visible hollows (Webb and Shine, 1997; Gibbons *et al.*, 2002; Koch *et al.*, 2008). We found no evidence of a similar trend occurring for nest boxes. Future studies could more closely investigate the relationship between structural tree attributes and nest box occupancy as recent research suggests that certain animal groups (e.g. hollow-nesting birds) may be particularly attracted to larger trees that have been enriched with nest boxes (Le Roux *et al.*, 2015a).

Landscape context had no significant effect on overall nest box occupancy, which is counter to others studies that have reported only limited occupancy of nest boxes in environments with an abundance of hollow-bearing trees (Smith and Agnew, 2002; Lindenmayer *et al.*, 2009). One explanation for our result is that temperate woodland habitats, like those in our study area, tend to support lower overall densities of hollow-bearing trees (7-17 hollow-bearing trees / ha) compared with habitats like temperate rainforests (13-27 hollow-bearing trees / ha; Gibbons and Lindenmayer, 2002). This may have resulted in more extreme differences in hollow availability and a greater discrepancy in nest box occupancy between unmodified and modified locations in other study environments compared to our own study location where hollow-bearing tree availability was more graded across the landscape contexts (Table 2). Some animals species are known to occupy nest boxes only in areas where natural hollows are abundance (Menkhorst, 1984). In our study, the sugar glider and the Australian owlet nightjar occupied nest boxes only in semi-natural reserves where the highest densities of hollow-bearing trees were recorded. Therefore, the probability of nest boxes being occupied may simply be due to the likelihood of a species being present and encountering nest boxes in a given environment. Similar rates of nest box occupancy across landscape types in our study are also likely due to the ubiquitous nature of common native and exotic species that predominately occupied nest boxes.

We found strong evidence that common adaptable native and exotic species exploit nest boxes in all landscape contexts investigated in our study. The European honey bee showed a preference for occupying nest boxes in urban built-up areas, which is somewhat unsurprising given that this generalist pollinator is known to exploit resources (e.g. flowering garden plants) in residential areas (e.g. Threlfall *et al.*, 2015). Nest boxes were rarely occupied by exotic birds especially in urban environments, which is counter to findings from other studies conducted in the same study area (Pell and Tidemann, 1997; Harper *et al.*, 2005; Grarock *et al.*, 2013). Recent eradication programs targeting exotic birds in suburban areas of Canberra (particularly the common myna) may explain lower than expected occupancy of nest boxes by exotic birds (Grarock *et al.* 2014). We found that the common brushtail possum (often regarded as a ‘native pest’ in urban areas) showed a strong preference for occupying nest boxes in urban environments, which was congruent with other studies (Harper *et al.*, 2005).

Considerations for management and biodiversity offsets

Where nest boxes are used to achieve no-net-loss of habitat as part of a biodiversity offset requirement (Lindenmayer *et al.*, 2009; Peste *et al.*, 2015), we suggest that the minimum compensation required for the unavoidable loss of each hollow-bearing tree should be multiple nest boxes with different entrance sizes (Lambrechts *et al.*, 2012; Rueegger *et al.*, 2013; Goldingay *et al.*, 2015; Lindenmayer *et al.*, 2015). A single large, hollow-bearing tree typically supports many hollows with a range of entrance sizes that provide a diversity of nesting opportunities for numerous species (Gibbons *et al.*, 2002; Koch *et al.*, 2008; Cockle *et al.*, 2011; Le Roux *et al.*, 2014a). Multiple nest boxes with different entrance sizes more accurately reflects the availability of natural hollows as they occur naturally at hollow-bearing trees (Lindenmayer *et al.*, 1991). We also caution against a 'one-size-fits-all' approach because this has the potential to exclude certain species from occupying nest boxes and enable others to potentially exploit nest boxes. This could result in an increase in the population size or range expansion of dominant or problematic species and further exacerbate shortages in natural hollows by increasing competition at limited nest sites (Pell and Tidemann, 1997; Lindenmayer *et al.*, 2009; von Post and Smith, 2015).

Some characteristics of hollows are difficult to replicate artificially, especially on a large scale (e.g. hollows that are very deep, shallow, wide, narrow or located very high). Hollow-bearing trees also provide other critical habitat structures (e.g. logs, dead branches, large living lateral branches, and peeling bark microhabitat) that many species depend on for survival and can take as long to form as natural hollows (Manning *et al.*, 2006; Lindenmayer *et al.*, 2013). Therefore, management and offset programs that only use nest boxes as replacement habitat for the loss of large trees are unlikely to benefit many species, including species with specialist hollow requirements or species that depend on other habitat structures provided by large trees.

We found that six common native and exotic species accounted for 89% of nest box occupancies and no species of conservation concern occupied nest boxes despite threatened hollow-nesting species occurring in our study area (e.g. superb parrot *Polytelis swainsonii*). Paradoxically, nest boxes are often employed to compensate threatened hollow-nesting species most at risk of being impacted by human activities (Goldingay and Stevens, 2009; Lindenmayer *et al.*, 2009). This is despite only limited empirical evidence demonstrating that targeted threatened species will occupy nest boxes in a capacity that can benefit local populations over the long-term (see Goldingay *et al.*, 2015). These efforts typically require nest box locations and designs to be highly targeted, which often only focus on a single threatened species or species group (e.g. Libois *et al.*, 2012; Rueegger *et al.*, 2013; Olah *et al.*, 2014).

A further consideration is the rapid rate of nest box attrition. Even within two years we recorded the loss of five nest boxes (3.5%). Nest box attrition (with a conservative estimated ‘lifespan’ of 10 years per nest box) may exceed the time it takes for some animal species to locate and occupy nest boxes (Lindenmayer *et al.*, 2009). In contrast, natural hollows likely persist over much longer time periods (Gibbons *et al.*, 2000; Ranius *et al.*, 2009). Efforts to maximise the durability of nest boxes over longer time periods could involve improvements to construction materials, attachment methods, and removing certain species (e.g. European honey bee hives) from nest boxes (Beyer and Goldingay, 2006; Goldingay *et al.*, 2015). The efficacy of nest box programs also needs to be balanced against the financial costs associated with monitoring, maintaining and replacing nest boxes over the long-term (McKenney and Lindenmayer, 1994; Harper *et al.*, 2005). In our study, the expense of construction materials, labour, travel and monitoring 144 nest boxes over two years was approximately AUD$ 13,608 ($94 per nest box ($40 for materials and $27 per year for monitoring)).

We recommend that, when used in isolation, nest boxes are unlikely to be effective management and biodiversity offset tools because: (1) the attributes of natural hollows and other habitat structures provided by hollow-bearing trees (e.g. logs) cannot be easily replicated; (2) there is a high probability that there will be a lack of equivalence between trees removed (losses) and nest boxes added (gains), both in availability (number of nest boxes added as compensation) and functionality (number of nest boxes occupied by targeted species); and (3) there is little confidence that nest boxes can effectively ameliorate the loss of natural hollows by providing long-term benefits for many hollow-dependant species, especially rare and threatened taxa that face the highest risk of population decline and extinction in the interim.

We encourage policymakers and managers to place a greater emphasis on mitigating and avoiding the loss of large, hollow-bearing trees. Priority should be given to retaining trees that support multiple hollows with a variety of entrance sizes and characteristics that likely benefit many species (Gibbons and Lindenmayer, 2002). As an example, new urban developments could be planned so that a greater proportion of existing trees are safely retained and managed in urban greenspace rather than simply being removed (Stagoll *et al.*, 2012; Barth *et al.*, 2015; Ikin *et al.*, 2015; Le Roux *et al.*, 2015b). Accelerating the formation of hollows by other means (e.g. carving out hollows with chainsaws), or creating nest boxes that more closely mimic the characteristics of natural hollows also still warrants further experimentation (Bull and Partridge, 1986; Lewis, 1998; Jansson *et al.*, 2009).

Based on our findings, we caution against the wide-scale implementation of nest box programs, which still require further research aimed at increasing their effectiveness. Nest box supplementation should be considered only as an interim management strategy undertaken in conjunction with other mitigation and avoidance tactics, such as limiting the removal of established hollow-bearing trees in modified environments. Manipulating nest box entrance size and placement in the landscape can effectively exclude or encourage occupancy by common hollow-nesting species, which could have other important implications for wildlife management (e.g. studying the breeding ecology of hollow-using species; Mainwaring, 2011; Wiebe, 2011; Björklund *et al.*, 2013). Nest boxes may also play a vital role in education and in improving ecosystem functioning even when occupied by common native and exotic species (e.g. crop pollination by European honey bees).

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Supporting information

Fig. S1. Photographs showing: (i) nest boxes constructed with different entrance sizes (20, 35, 55, 75, 95 and 115 mm, diameter); (ii) a nest box installed directly onto a tree using a wooden panel (backboard) and galvanised hardware (Zenith M10 coach bolts, 75-100mm) that is being inspected using a wireless camera mounted onto an extension pole; (iii) a common brushtail possum emerging from a nest box; (iv) recently hatched crimson rosella chicks inside a nest box; and (v) European honeybees congregating on a nest box.

Table S1. Summary of generalised linear mixed model (GLMM; logistic regression) results, testing the effects of nest box entrance size, tree size and landscape context on nest box occupancy (n = 140).

Fitted terms		Coefficient (estimate)	Standard error	Wald	Degrees of freedom	*P*-value
Intercept (constant)		-0.57	0.79			
Nest box entrance size (mm):	20 (reference level)	0.00	± 0.82 (mean)	50.13	5	<0.001*
	35	-1.15				
	55	1.59				
	75	1.99				
	95	3.87				
	115	2.56				
Tree size (DBH):	Small (reference level)	0.00	± 0.68 (mean)	0.01	2	0.99
	Medium	-0.04				
	Large	0.02				
Landscape context:	Reserve (reference level)	0.00	± 0.83 (mean)	1.18	3	0.76
	Pasture	0.41				
	Urban parkland	0.84				
	Urban built-up	0.16				
Tree identity (random)		2.23	1.02			

Table S2. Summary of multinomial model selection based on ranked Akaike's Information Criteria (AIC) values.

Rank	Model	AIC	Δ AIC	Log-likelihood	Weight
1	Nest box entrance size + landscape context	256.75	0.00	-92.37	0.99
2	Nest box entrance size + tree size + landscape context	265.39	8.64	-88.67	0.01
3	Nest box entrance size	270.63	13.88	-111.31	0.00
4	Nest box entrance size + tree size	282.00	25.25	-109.00	0.00
5	Nest box entrance size + (landscape context x tree size)	293.18	36.43	-78.59	0.00
6	Landscape context + (nest box entrance size x tree size)	325.73	68.98	-78.86	0.00
7	Landscape context	347.43	90.68	-157.71	0.00
8	(Landscape context x tree size) + (nest box entrance size x tree size)	349.28	92.53	-66.64	0.00
9	Landscape context + tree size	359.36	102.61	-155.65	0.00
10	(Landscape context x tree size) + (landscape context x tree size)	370.70	113.95	-57.34	0.00
11	Landscape context x tree size	387.81	131.06	-145.90	0.00
12	(Nest box entrances size x landscape context) + (nest box entrance size x tree size)	404.43	147.68	-58.24	0.00
13	(Landscape context x tree size) + (nest box entrance size x landscape context) + (nest box entrance size x tree size)	423.88	167.13	-43.49	0.00
14	Nest box entrance size x tree size x landscape context	645.63	388.88	-38.81	0.00

Table S3. Summary of multinomial logistic regression results (coefficient ± standard error), testing the effects of entrance size and landscape context on nest box occupancy (n = 133) by common fauna (species that occupied ≥ 5% of nest boxes). Response categories included occupancy by either: the common brushtail possum, exotic birds, common native birds, or the European honey bee. 'No occupancy' of nest boxes was included as an additional response.

Significant model terms		No occupancy (reference level)	The common brushtail possum	Exotic birds	Common native birds	European honey bee
Nest box entrance size (mm)	20 (reference level)	0.00 ± 0.00	-20.04 ± 0.64	-18.43 ± 0.57	-21.48 ± 0.69	-0.09 ± 0.69
	35	0.00 ± 0.00	-18.17 ± 0.00	-3.73 ± 0.00	-3.19 ± 0.00	-1.58 ± 0.76
	55	0.00 ± 0.00	16.93 ± 0.98	19.28 ± 0.65	20.67 ± 0.62	-1.19 ± 0.99
	75	0.00 ± 0.00	17.85 ± 0.73	18.22 ± 0.69	21.12 ± 0.58	-18.39 ± 0.00
	95	0.00 ± 0.00	20.99 ± 0.66	17.09 ± 0.98	-0.18 ± 0.00	-18.72 ± 0.00
	115	0.00 ± 0.00	20.35 ± 0.59	16.92 ± 0.95	19.02 ± 0.95	-19.40 ± 0.00
Landscape context	Reserve (reference level)	0.00 ± 0.00	-20.04 ± 0.64	-18.43 ± 0.57	-21.48 ± 0.69	-0.09 ± 0.69
	Pasture	0.00 ± 0.00	-1.18 ± 1.02	0.11 ± 0.95	1.34 ± 1.13	-1.01 ± 1.02
	Urban parkland	0.00 ± 0.00	1.64 ± 1.09	-18.70 ± 0.00	0.38 ± 1.09	-0.53 ± 0.93
	Urban built-up areas	0.00 ± 0.00	1.89 ± 1.12	-0.83 ± 1.09	-16.38 ± 0.00	1.21 ± 0.87

Table S4. Percentage (mean ± SEM) of nest boxes occupied (n = 133) by common fauna (species that occupied ≥ 5% of nest boxes) as derived from multinomial logistic regression results testing the effects of entrance size and landscape context. Response categories included occupancy by either: the common brushtail possum, exotic birds, common native birds, or the European honey bee. ‘No occupancy’ was included as an additional response.

Significant model terms		No occupancy	The common brushtail possum	Exotic birds	Common native birds	European honey bee
Nest box entrance size (mm)	20	54.2 ± 10.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	45.8 ± 10.3
	35	81.8 ± 8.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	18.2 ± 8.4
	55	30.0 ± 10.5	5.0 ± 5.0	35.0 ± 10.9	20.0 ± 9.2	10.0 ± 6.9
	75	36.8 ± 11.3	15.7 ± 8.6	15.7 ± 8.6	31.5 ± 10.9	0.0 ± 0.0
	95	22.2 ± 10.1	72.2 ± 10.9	5.5 ± 5.5	0.0 ± 0.0	0.0 ± 0.0
	115	27.7 ± 10.8	61.1 ± 11.8	5.5 ± 5.5	5.5 ± 5.5	0.0 ± 0.0
Landscape context	Reserve	44.8 ± 9.4	17.2 ± 7.1	17.2 ± 7.1	6.9 ± 4.7	13.8 ± 6.5
	Pasture	53.1 ± 8.9	9.3 ± 5.2	15.6 ± 6.5	15.6 ± 6.5	6.2 ± 4.3
	Urban parkland	45.2 ± 9.1	32.2 ± 8.5	0.0 ± 0.0	12.9 ± 6.1	9.6 ± 5.4
	Urban built-up areas	31.0 ± 8.7	34.4 ± 8.9	6.8 ± 4.7	0.0 ± 0.0	27.6 ± 8.4