LETTER

Large trees are keystone structures in urban parks

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Abstract

Large trees are considered keystone structures in agricultural and forestry production landscapes, but research demonstrating this in urban landscapes is urgently needed. If large trees are keystone structures in urban parks, it is imperative that this is recognized in policy to ensure their ongoing existence. We studied the role of large native trees for birds in urban parks in Canberra, Australia. We found that (1) large trees had a consistent, strong, and positive relationship with five measures of bird diversity, and (2) as trees became larger in size, their positive effect on bird diversity increased. Large urban trees are therefore keystone structures that provide crucial habitat resources for wildlife. Hence, it is vital that they are managed appropriately. With evidence-based tree preservation policies that recognize biodiversity values, and proactive planning for future large trees, the protection and perpetuation of these important keystone structures can be achieved.

Introduction

The worldwide decline of mature trees has recently become a topic of conservation concern (Manning *et al.* 2006; Vesk & Mac Nally 2006; Gibbons *et al.* 2008; deMars *et al.* 2010; Fischer *et al.* 2010a; Rolo & Moreno 2011). Their loss will have negative consequences for biodiversity and associated ecosystem services (Fischer *et al.* 2009, 2010a, and references therein).

Large trees are considered keystone structures because they provide "resources, shelter, or 'goods and services' crucial for other species" (Tews *et al.* 2004, p. 86; also see Manning *et al.* 2006; Fischer *et al.* 2010a). They provide critical habitat for a range of taxa, including bats (e.g., Lumsden & Bennett 2005; Fischer *et al.* 2010a, b), ground-dwelling, and arboreal mammals (e.g., Gibbons & Lindenmayer 2002; Mazurek & Zielinski 2004; Lindenmayer *et al.* 2011), birds (e.g., Poulson 2002; Loyn & Kennedy 2009; deMars *et al.* 2010; Seymour & Dean 2010; Stagoll *et al.* 2010), and invertebrates (e.g., Sirami *et al.* 2008; Carpaneto *et al.* 2010). Large trees are important for the production of coarse woody debris (Killey *et al.* 2010) and provide a distinct microclimate, with increased soil nutrients, plant species richness and structural complexity (Manning *et al.* 2006). Furthermore, large trees fulfill a range of landscape-scale ecological functions, including increasing habitat connectivity, which may facilitate species' range expansions and thus capacity to adapt to climate change (Manning *et al.* 2009). In addition to these biological functions, large trees are also important socially, culturally, and aesthetically (Jim 2004, 2005).

Research on the value of large trees has primarily been undertaken in forestry production areas (e.g., Lindenmayer & Franklin 1997; Mazurek & Zielinski 2004; Gibbons *et al.* 2010; Lindenmayer *et al.* 2011) and, more recently, agricultural landscapes (e.g., Gibbons & Boak 2002; Sirami *et al.* 2008; deMars *et al.* 2010; Seymour & Dean 2010). From this research, it can be predicted that large trees should also play an important function in urban landscapes. However, most previous work has focused on their role in atmospheric pollution and carbon dioxide reduction, energy reduction, stormwater runoff mitigation, and provision of aesthetic (e.g., personal well-being, recreation, and property value) benefits (Jim 2004; Millward & Sabir 2011, and references therein). In comparison, the decline of large urban trees and their value to biodiversity has received much less attention (but see Jim 2005; Grigg *et al.* 2009). Recent work, however, in Italy (Carpaneto *et al.* 2010), Mexico (Ortega-Alvarez & MacGregor-Fors 2010), and Australia (Harper *et al.* 2005) suggests that large trees provide important habitat structures for a variety of urban wildlife. However, the protection and perpetuation of large trees in urban areas sometimes conflicts with other urban policies, such as public safety measures (e.g., Carpaneto *et al.* 2010) and sustainable growth strategies that increase residential density (Pauleit *et al.* 2005). Therefore, more research demonstrating the crucial value of large trees in urban areas is urgently needed.

We present a case study on the value of large trees in urban parks for birds. We asked: (1) do large trees have a consistent, positive, and strong effect on bird diversity? We investigated five measures of bird diversity directly relevant to the keystone role of large trees: (i) bird species richness, and (ii) abundance, as an indication of the availability and quality of habitat resources for birds; (iii) incidence of breeding, as an indication of the fitness (reproduction and survival) of individual species; (iv) woodland-dependent species richness; and (v) community structure, as an indication of how large trees can alter species assemblages. In addition, we asked: (2) how large do trees need to be to have an effect on bird diversity? We expected that as the minimum trunk diameter threshold for "large" trees increases, the strength of the effect of these trees on the various measures of bird diversity also would increase.

Methods

Study area

We conducted our study in Canberra, Australian Capital Territory (ACT), in southeastern Australia. Canberra is approximately 800 km^2, and has a population of 362,000 people. Population density is approximately 452 people per km^2 (ABS 2010). The city is known as the "Bush Capital" and there is substantial urban tree cover across public and private land. Within public land,

Figure 1 (A) Example of a typical urban park with a large tree (Burrinjuck Crescent Neighborhood Park, Duffy, Canberra, Australia). (B) Example of planned landscaping separating children's play area (foreground) and large trees (Heritage Park, Forde, Canberra, Australia).

there are several categories of urban parkland, ranging from large formally managed town parks to informal district parks, small neighborhood parks, pedestrian parkland and laneways, and informal-use sporting fields (ACT Government 2006). We chose to focus on neighborhood parks, which are typically used for recreation and often include playground facilities (Figure 1A). Neighborhood parks are located in residential areas, are usually 0.25–2 ha in area, and are spaced so that every dwelling is generally within 400 m of a park (ACT Government 2006). As such, these parks may provide a continuum of wildlife habitat throughout urban areas, and their appropriate management is important for urban conservation. We identified neighborhood parks that were between 0.5 ha and 2 ha, contained native trees of the genus *Eucalyptus*, were >500 m from other parks, >250 m from nature reserves, and in suburbs where the median residential block size was between 200 m^2 and 1,100 m^2. We placed a 50-m radius (0.8 ha) site at the geographic centroid of each park. We then excluded parks that had <60% of total site area (i.e., <0.5 ha) within the park boundaries. This selection process gave us sites in 109 neighborhood parks, from an original total pool of 337 parks.

Park trees and vegetation

We measured the trunk diameter at breast height (DBH; 1.3 m above ground level) of all live eucalypt trees within the site. For trees with multiple stems at breast height, we measured the diameter of each stem, and used the summed basal area to calculate the equivalent diameter for a single-stemmed tree with the same basal area at breast height (following Fischer *et al.* 2009). We then aggregated this data to the site scale by calculating the number of "large" eucalypt trees per hectare. There are several ways to define large trees in the academic literature and management policies, ranging from greater size and age compared to neighboring trees (e.g., Mazurek & Zielinski 2004; Loyn & Kennedy 2009) to specified minimum trunk diameters (e.g., Harper *et al.* 2005; deMars *et al.* 2010). Because of these differing definitions, we chose not to explicitly define large trees but instead to investigate a range of minimum trunk diameters. We therefore calculated the number of eucalypt trees per hectare in each site with a DBH >0 cm (all trees) and the number of trees per hectare in 10 other minimum diameter size classes, ranging from DBH >10 cm to DBH >100 cm. These measures corresponded to a conservative estimate of tree age, as the age of eucalypts is positively associated with tree diameter (Koch *et al.* 2008).

We also recorded within each site: (1) the total number of trees per hectare (of all species), (2) the proportion that were eucalypts, (3) the presence of shrubs, (4) the percentage cover of leaf litter, and (5) the percentage cover of grass. We ran a principal components analysis on these five variables to characterize the vegetation of each park, log-transforming percent shrub and leaf litter cover before analysis because these variables were highly skewed (Table S1). We used this principal component (vegetation index) to adjust for differences in park vegetation cover between sites in later analyses.

Birds

We surveyed each site for birds using 10-minute 50-m radius point counts. We conducted two separate morning surveys in spring 2010, and avoided rainy or windy days. We recorded the presence and abundance of all species seen or heard, as well as the incidence of breeding by any species (see Table S2 for breeding definitions). All of the parks had open vegetation and clear lines of sight; we were therefore confident that we detected all birds present during our surveys. We used a list developed by Birds Australia to identify bird species associated with woodland habitats (Silcocks *et al.* 2005) to determine woodland species richness. Finally, we performed a correspondence analysis (CA) of species presence/absence data to summarize the community structure of birds at each site. This ordination technique scores species on the basis of the sites were they occur (CA species scores) and scores sites on the basis of the species they contain (CA site scores), and maximizes the correlation between the two scores. This gradient of CA species scores was positively correlated with CA site scores ($R = 0.49$), and so we used the CA site scores as a proxy for community composition.

Data analysis

To assess whether large trees were having an effect on bird diversity, we fitted generalized linear models for five bird responses: species richness, average abundance, probability of breeding, woodland species richness, and community composition. For each of these responses, we fitted 11 separate models, with a different value of "trees per hectare" for each DBH size class, ranging from DBH >0 cm (all trees) to DBH >100 cm (55 models in total), to investigate whether the strength of the effect of large trees increased with increasing trunk diameter. To account for differences in vegetation between sites, we fitted the vegetation index first in the models (i.e., response = vegetation index + trees per hectare). We fitted models with a Poisson error distribution and log link function, except for the models for probability of breeding (binomial distribution and logit link function) and the community composition models (normal distribution and identity link function). Before fitting the models, we used spline correlograms to confirm that there was no spatial autocorrelation between sites. For each of the bird responses, we examined and compared the estimated effect sizes (regression coefficients) and fitted models. We considered the effect sizes to be strong when the 95% confidence interval did not include 0.0. To aid our model comparisons, we ranked the models using the Akaike Information Criterion (AIC; Burnham & Anderson 2002).

Results

We recorded 44 bird species (Table S2), with an average of 7.8 (± 2.6 standard deviation) species, 11.5 (±6.2) individual birds and 3.5 (±1.5) woodland species per site. We recorded the incidence of breeding at 49% of sites. The gradient in community composition ranged from species that were smaller-bodied and shrub-dependent to species that were larger-bodied and tree-dependent (Figure S1). We measured 3,300 eucalypt trees, with an average of 49.1 trees per ha (±39.6).

The number of eucalypt trees per hectare had a positive effect on bird richness (Figure 2A), average abundance (Figure 2B), probability of breeding (Figure 2C), woodland species richness (Figure 2D), and community composition scores (Figure 2E) in 52 of the 55 models we constructed (Table S3). In contrast, we did not find a strong or consistent effect of the site vegetation index on any of the bird responses (Figure S2).

The effect size of trees per hectare was weak (i.e., the confidence interval included 0.0) until trees reached a minimum threshold diameter (Figure 2, Table S3). We found that the effect size was weak until trees were >50 cm for species richness, >50 cm for average abundance, >40 cm for probability of breeding, >40 cm for woodland species richness, and >50 cm for community composition. For all bird responses, the best-ranked models (lowest AIC) were those where tree diameters were large (DBH at least 80 cm; Table S3).

As the diameter of the trees increased, the magnitude of the effect size also increased (Figure 2, Table S3). When compared to increases after the addition of five random trees to a park, the addition of five trees >100 cm increased species richness by 157%, average abundance by 91%, probability of breeding by 158%, and woodland species richness by 301%.

Discussion

Large trees are considered keystone structures in agricultural and forestry production landscapes because they are crucial for ecosystem function and provision of habitat resources (Tews *et al.* 2004). Our study is the first to explicitly demonstrate that large trees are also keystone structures in urban parks. This is because they have a consistent, positive, and strong relationship with bird richness, average abundance, presence of breeding, woodland species richness, and community composition. Furthermore, we confirmed that as trees became larger in size, their positive effect on bird diversity also increased. To our knowledge, this finding has not been previously demonstrated directly for bird fauna, although several studies have identified a similar pattern between large trees and structural characteristics (e.g., hollows: Lindenmayer *et al.* 1993; Harper *et al.* 2005; coarse woody debris: Killey *et al.* 2010).

Large trees provide structural complexity not offered by smaller trees. For example, Mazurek & Zielinksi's (2004) study of Californian commercial forest found that young redwood (*Sequoia sempervirens*) trees lacked large horizontal limbs, basal hollows, and cavities, which probably lowered their attractiveness to wildlife compared with older and larger trees. In Australia, 15% of terrestrial vertebrates use eucalypt hollows (Gibbons & Lindenmayer 2002), and Harper *et al.* (2005) found that the probability of live eucalypt trees having at least one hollow increased as trunk diameter increased. Similarly, in France, Sirami *et al.* (2008) found that the availability of large pieces of dead wood, critical habitat for saproxylic beetles, was positively correlated with tree size. Large trees also provide disproportionate quantities of flowers, pollen, nectar, seed set, mistletoe, and hanging bark, which are important food and microhabitat resources for a range of invertebrate and vertebrate species (Lindenmayer & Franklin 1997, and references therein). Furthermore, within the urban context in particular, large trees may provide places of concealment and act as essential refuges from human disturbances, such as recreation and traffic noise (Fernandez-Juricic *et al.* 2001).

More specific research quantifying the importance of large trees in urban areas for wildlife would be valuable for urban management, particularly if focused on a range of vertebrate and invertebrate taxa. Further research on how the role of large urban trees changes with different urban settings and/or urban densities is also needed, especially for mobile taxa such as birds that are affected by local landscape context (Lim & Sodhi 2004; Sattler *et al.* 2010).

Because large urban trees provide important habitat resources for wildlife, it is vital that they are managed appropriately. The loss of large trees from urban settings may have far-reaching ecological consequences that may undermine other biodiversity conservation measures. Harper *et al.* (2005, p. 187) for example, concluded that a lack of large hollow-bearing trees was "possibly the greatest threat to the short-term (<20 years) ecological sustainability" of urban remnants within their study region in southeastern Australia. This is particularly pertinent in urban areas where management policies often cause trees to be felled or extensively pruned before they reach their full biological potential (Jim 2004, 2005; Carpaneto *et al.* 2010), thereby limiting their value to wildlife. For example, we found that species richness increased by approximately 10% with the addition of five >50 cm trees but by over 150% with the addition of five >100 cm trees. For richness of woodland dependent species, the increase was over 300%. On the basis of these results, we argue for the preservation of very large trees (>100 cm) in urban areas, and their prioritization over other management considerations when policies conflict. Risk posed by large, old trees should be managed by strategies other than tree removal, for example fencing or landscaping (Figure 1B).

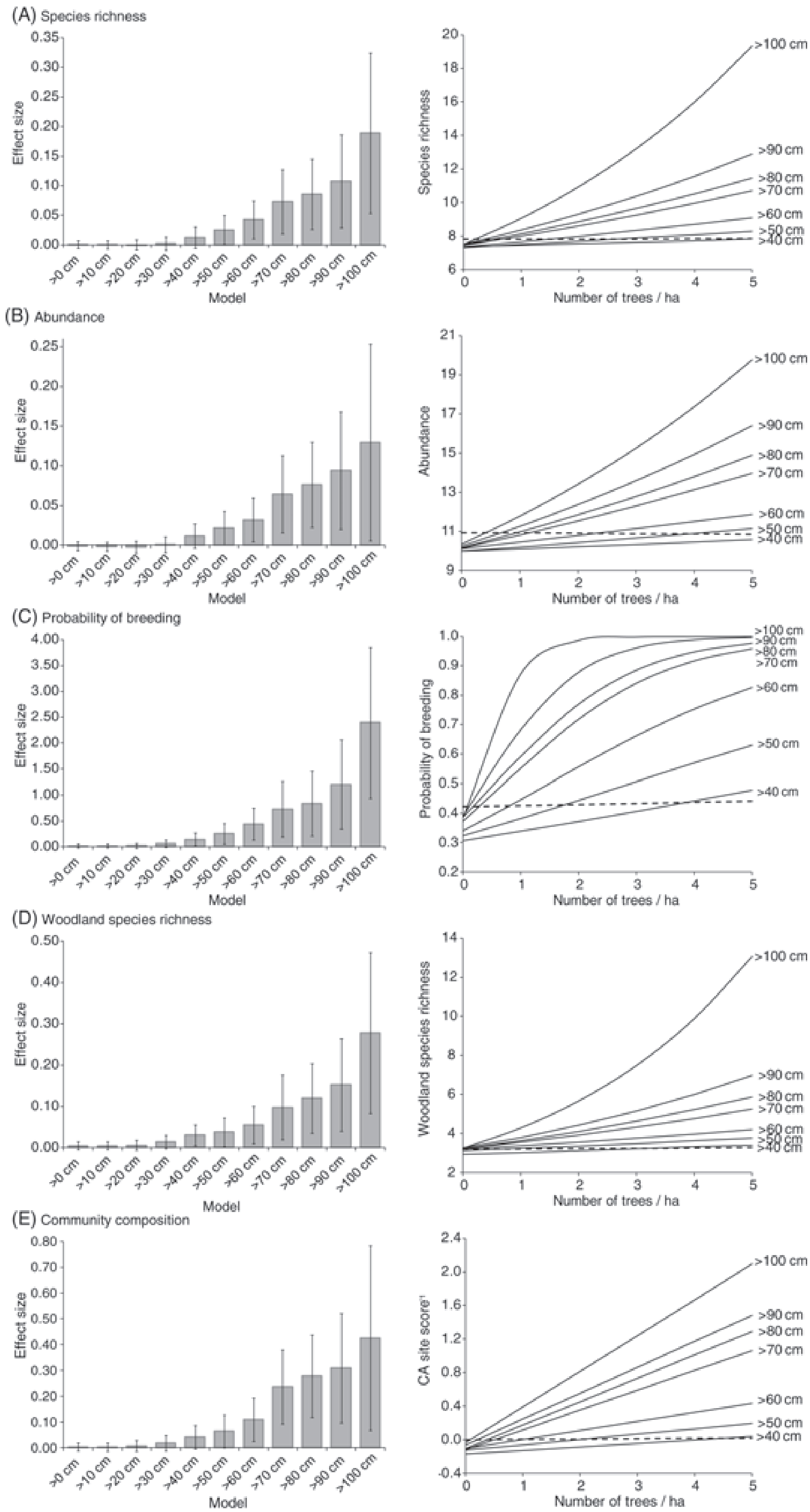

Figure 2 Effect sizes for trees per hectare (± 95% confidence intervals) and estimated relationships from generalized linear models (response = vegetation index + trees per hectare) of (A) species richness, (B) average abundance, (C) probability of breeding, (D) woodland species richness (see Table S2 in the online supporting information), and (E) community composition (see Figure S1). Separate models were fitted for each diameter at breast height (DBH) size class, ranging from DBH >0 cm (all trees) to DBH >100 cm (see Table S3). Fitted models were obtained by fixing the value of the vegetation index at its mean. Dashed lines indicate the fitted model for DBH >0 cm.

Table 1 Selected examples of urban tree protection policies worldwide that are based on physical criteria

Region	Managing authority	Policy	Physical criteria for protection
North America	Redwood City, California, USA	Tree Preservation Ordinance	Any private property tree >30-cm trunk diameter
	City of Austin, Texas, USA	Tree and Natural Area Preservation Ordinance	Any tree >50-cm trunk diameter
	City of Victoria, British Columbia, Canada	Tree Preservation Bylaw (No. 05–106)	Listed native species >50-cm height, listed native species >60-cm trunk diameter, and any private property tree >80-cm trunk diameter
	City of Kingston, Ontario, Canada	Tree Bylaw (No. 2007–170)	Any tree >15-cm trunk diameter
Europe	Bratislava, Slovakia	Act of the National Council of the Slovak Republic No. 287/1994: On the Preservation of Nature And Landscape	Any tree >50-cm trunk diameter
	City of Dublin, Ireland	Zoning Code (§153.141)	Any tree >15-cm trunk diameter
Asia	Singapore	Parks and Trees Act 1996	Any tree >30-cm trunk diameter
Australia	City of Sydney	Tree Preservation Order 2004	Any tree >5-m height or >10-cm trunk diameter or >30-cm aggregated diameter (multiple trunks)
	Canberra, Australian Capital Territory	Tree Protection Act 2005	Any tree >12-m height, >12-m crown width, or >50-cm trunk diameter (this can be split between multiple trunks)

Our results conflict with existing tree protection policy in urban open space in many jurisdictions. We found that trees as small as 40 cm in diameter can have a strong positive effect on bird diversity, which is smaller than minimum sizes prescribed by many managing authorities, including in North America, Europe, Asia, and Australia (Table 1). In our study area, government law regulates only the removal of trees >50 cm in diameter, so that 457 park trees 40–49 cm in diameter (14% of all trees that we measured) do not receive formal protection. Similar numbers of trees may be at risk in other cities worldwide where the physical criteria for tree regulation focus on larger trunks (Table 1). Tree preservation laws, therefore, may not be providing adequate protection for a large number of important trees. We suggest that physical criteria for protection as part of tree preservation policies should be evidence-based and regularly reviewed and that the value of large trees for biodiversity be explicitly acknowledged.

Finally, our findings reiterate the importance of proactively planning for future large trees (Jim 2004). It takes many decades for a newly planted sapling to become a large tree (Koch *et al.* 2008). Within urban areas, it is thus critical for long-term sustainability to actively manage for a diversity of tree ages, so that younger trees may eventually replace mature and over-mature trees (Harper *et al.* 2005; Millward & Sabir 2011). These younger trees may also provide important structural habitat for wildlife complementing that provided by large trees (Munro *et al.* 2011).

In conclusion, we have unequivocally demonstrated that large trees are of critical value in urban areas as keystone structures. Worldwide, large trees are declining in a range of human-managed ecosystems, including agricultural areas (Gibbons *et al.* 2008), forestry production regions (Gibbons *et al.* 2010), and urban landscapes (Jim 2005; Grigg *et al.* 2009). Negative consequences for biodiversity have been predicted as a result of this decline (Fischer *et al.* 2009; Fischer *et al.* 2010a, and references therein). This threat is exacerbated by the substantial amount of time needed before younger trees are capable of providing the same level of habitat resources as large trees (Lindenmayer *et al.* 1993; Harper *et al.* 2005). For the best possible conservation of large trees and their ongoing existence into the future, it is urgent that the value of large trees for biodiversity is recognized in urban management and planning policies. With evidence-based tree preservation policies and the specific recognition that large trees are critical for biodiversity, the protection and perpetuation of these important keystone structures could be achieved.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1: Summary of correspondence analysis (CA) scores for species.

Figure S2: Effect sizes for vegetation index (± 95% confidence intervals) from generalized linear models (response = vegetation index + trees per hectare) of (A) species richness, (B) average abundance, (C) probability of breeding, (D) woodland species richness (see Table S2), and (E) community composition (see Figure S1).

Table S1: Summary of principal components analysis (vegetation index).

Table S2: Complete list of observed bird species. Nomenclature is taken from Christidis & Boles (2008) and woodland species classification follows Silcocks *et al.* (2005).

Table S3: Generalized linear models (response = vegetation index + trees per hectare) for (A) species richness, (B) average abundance, (C) probability of breeding, (D) woodland species richness, and (E) community composition.

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