



The influence of patch area and connectivity on avian communities in urban revegetation

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ABSTRACT

Landscape restoration through revegetation is being increasingly used in the conservation management of degraded landscapes. To effectively plan restoration programs information is required on how the landscape context of revegetation influences biodiversity gains. Here, we investigate the relative influence of patch area and connectivity on bird species richness and abundance within urban revegetation patches in Brisbane, Australia. We carried out bird surveys at 20 revegetation sites, and used hierarchical partitioning and model selection to test the relative importance of patch area (the area of revegetation including all directly connected remnant vegetation) and landscape connectivity (the vegetated area connected by less than 10 m, 20 m, 30 m, 40 m and 50 m cleared gaps). We controlled for a number of possible confounding variables within the hierarchical partitioning procedure. Both the hierarchical partitioning and model selection procedures indicated that connectivity had an important influence on bird species richness. Patch area in combination with connectivity were important influencing factors on overall bird abundance. We also carried out the hierarchical partitioning procedure for bird abundance data within a range of feeding guilds, yielding results specific to species groups. Overall our data suggest that greater connectivity enhances the habitat area that colonists can arrive from (resulting in greater species richness), whereas increased patch area allows for increased abundance by expanding the habitat available to species already present in a patch. A combined approach where connectivity and overall habitat area is enhanced across the landscape is likely to be necessary to meet long-term conservation objectives.

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1. Introduction

In many regions vegetation cover is so depleted that reserve systems of existing remnants will be insufficient to achieve any real conservation outcome (Vesk and Mac Nally, 2006). The total amount of vegetation that remains in these degraded regions limits the potential population size of many species, and reduced connectivity among remnants can hamper dispersal (Hanski, 1994). Both factors are known to increase the local and regional extinction risk of a species (Gaggiotti and Hanski, 2004; Woodruff, 1990). Landscape restoration through revegetation is becoming an increasingly popular tool in the conservation management of highly degraded landscapes (e.g. Gondwana Link in south-western Australia, Gondwana Link Coordination Unit, 2009; Brisbane city's 2 Million Trees Project, Brisbane City Council, 2009). Revegetation can be used to reduce the extinction risk of species by creating new habitat and also through enhancing connectivity, effectively 'recon-

structing functioning landscapes' (Recher, 1999; Vesk and Mac Nally, 2006). Revegetation is an especially powerful tool in urbanising areas where habitat loss can be extensive across large parts of the landscape, and remaining vegetation is often rendered isolated and degraded (Rickman and Connor, 2003).

When planning revegetation projects in urban areas, there are two broad alternatives. First, the area of existing vegetation patches could be increased, and second landscape connectivity could be improved by joining patches together. The merits of these alternatives are unclear because the relative roles of landscape connectivity and patch area in enhancing the biodiversity value of revegetation projects are poorly understood. This is because few studies have empirically investigated how landscape configuration influences local-level colonisations; rather, research has focused on how landscape factors influence wildlife population extinctions (e.g. Burke, 1989; Martensen et al., 2008; Sekercioglu, 2007). This lack of empirical evidence is an important knowledge gap because revegetation is an expensive and long-term commitment; this is particularly so in urban landscapes where the cost of land acquisition or reclamation can be extremely high (Cavailles and Wavresky, 2003). Basic guidelines are required to ensure the

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effective use of this powerful and potentially highly manipulable means to restore ecosystems and enhance their conservation value (Thomson et al., 2007).

The question of where to direct revegetation efforts is one of the most challenging and pivotal issues for the design of revegetation programs (Vesk and Mac Nally, 2006), and the answer is likely to be complex due to the variety of species, vegetation considerations and landscape contexts to consider (Lindenmayer et al., 2010; Mac Nally and Horrocks, 2002; Westphal et al., 2007). Ideally, metapopulation models, population viability analysis and gap crossing analysis would be used to assess how a species of interest might respond to alternative possible landscape configurations (Westphal et al., 2003). However, such an approach is likely to be impractical in urban systems where landscape change is so extensive, and the opportunities for ecological reconstruction are limited. Furthermore, such a species specific approach is likely to be expensive and time consuming. Metapopulation theory offers some broad predictions that are potentially useful for making some generalisations, namely that extinction rates will be influenced primarily by patch area, while colonisation rates depend on connectivity (Etienne et al., 2004; Verboom et al., 1991). If these predictions were extended to the community level within revegetation, we might expect that connectivity has a greater influence on species richness owing to a greater number of colonisations, and with increased patch size we might expect more robust and healthy populations (reflected by greater overall abundance).

Local level empirical research in remnant vegetation shows mixed results when comparing the relative importance of connectivity and patch area, with some studies finding that patch area is the best predictor of bird species richness in remnant vegetation (Drinnan, 2005), while others have shown connectivity is a better predictor (Martensen et al., 2008). Variation in the results of these studies is perhaps driven by the amount of total available habitat in the landscape (Martensen et al., 2008), and is also likely to be influenced by the scale of study. Connectivity may become more important where little habitat is available, enabling species to exploit multiple patches (Martensen et al., 2008). Conversely, as habitat availability increases the importance of connectivity will decline. Revegetation in urban environments presents an ideal opportunity to assess empirically the relative importance of patch area and connectivity for species colonisations within an otherwise relatively impermeable landscape.

Here we assess the relative importance of total patch area and connectivity (where these measures include existing adjacent or connected remnant vegetation) on the richness and abundance of bird assemblages within the revegetation itself. We account for variation in vegetation complexity, age of the stand and overall levels of urbanisation surrounding the patches. These are all factors that influence bird communities within revegetation or urban vegetation (Cunningham et al., 2007; Freudenberger et al., 2004; Luck, 2007; Munro et al., 2007; Vesk et al., 2008). Our study sites are a series of active urban revegetation projects within Brisbane city (Southeast Queensland, Australia), initiated at various stages over the past 25 years, that have different levels of associated connectivity and total vegetation area.

2. Methods

2.1. Study area and bird surveys

The city of Brisbane, Australia, has an estimated human population of 1.04 million (Queensland Government, 2009). Revegetation projects have been carried out for at least 25 years within the region by local government and community groups as part of a waterways and greening plan (Brisbane City Council, 2008). We identified 20

revegetation sites between 1.5 and 2.5 ha in size, and estimated the age of each stand through personal communication with people involved in the programs; the stand ages range between 7 and 25 years. The revegetation was mixed canopy species woodland with shrubby understorey. These sites were all located in suburban areas, and spanned a range of human population densities and locations across the city (Fig. 1). All revegetation sites are under active management by local community groups whose activities include, for example, weed removal and tree care.

At each site, we made four repeat 20 min transect bird surveys, spread across the local bird breeding season months of October–December 2008, between 0500 h and 0900 h (total of 80 surveys). Transect routes allowed exhaustive coverage of the revegetated area, enabling the observer to walk within 25 m of all parts of the patch. All birds seen or heard within the revegetated area were recorded. Double counting of birds was considered a minor issue as the observer was continuously on the move (Gregory et al., 2004). Birds flying over the survey area were ignored with the exception of aerial feeders (e.g. swallows, woodswallows, raptors), and birds outside the revegetation patch were ignored even if detected from the transect. To account for the slight variation in transect area, this was included as a potential explanatory variable in the hierarchical partitioning analysis described below as 'Revege area'. For analysis purposes, bird abundance was the mean number of individuals counted across all surveys at a site. Species richness was the sum total of bird species recorded within each survey site.

To investigate how landscape and vegetation variables influenced the bird assemblage, we used information from the Handbook of Australian, New Zealand and Antarctic Birds (Marchant and Higgins, 1990, 1993; Higgins and Davies, 1996; Higgins, 1999, 2006; Higgins et al., 2001; Higgins and Peter, 2002) to assign each species detected in the surveys to a feeding guild (Table 1; see Supplementary material for a list of species and their feeding guild).

2.2. Variables measured

A number of factors that could potentially explain variation in bird species richness or abundance within revegetation were measured for use in the data analysis. These are described below.

2.2.1. Vegetation characteristics

Vegetation composition and complexity are important predictors of bird species diversity in revegetated areas (Vesk and Mac Nally, 2006), so we included them as covariates in this study. To characterise these variables, we placed a 50 m transect within each patch and surveyed to 3 m both sides of this line, giving a total survey area of 300 m². Within this transect we noted the identity of every woody stemmed plant species, as well as the diameter at breast height of each stem. We also recorded the species and height of all ground, shrub, and canopy cover plants whose foliage intersected the 50 m transect line at 2 m intervals, and converted this to vegetation percentage cover estimates. The resulting vegetation variables were:

- (i) woody plant species richness per 300 m²;
- (ii) woody stem density per 300 m²;
- (iii) overall tree density per 300 m²;
- (iv) average and total woody stem basal area per 300 m²;
- (v) percentage vegetation cover estimates (sub-canopy/canopy, >5 m height; shrub, 1–5 m height; grass/herb, 0–1 m height; ground cover, 0 m height).

We simplified these vegetation characteristics into fewer explanatory variables to generate a more parsimonious description of vegetation complexity, using R Version 2.2 (R Development Core Team, 2005). We constructed a Bray–Curtis similarity matrix

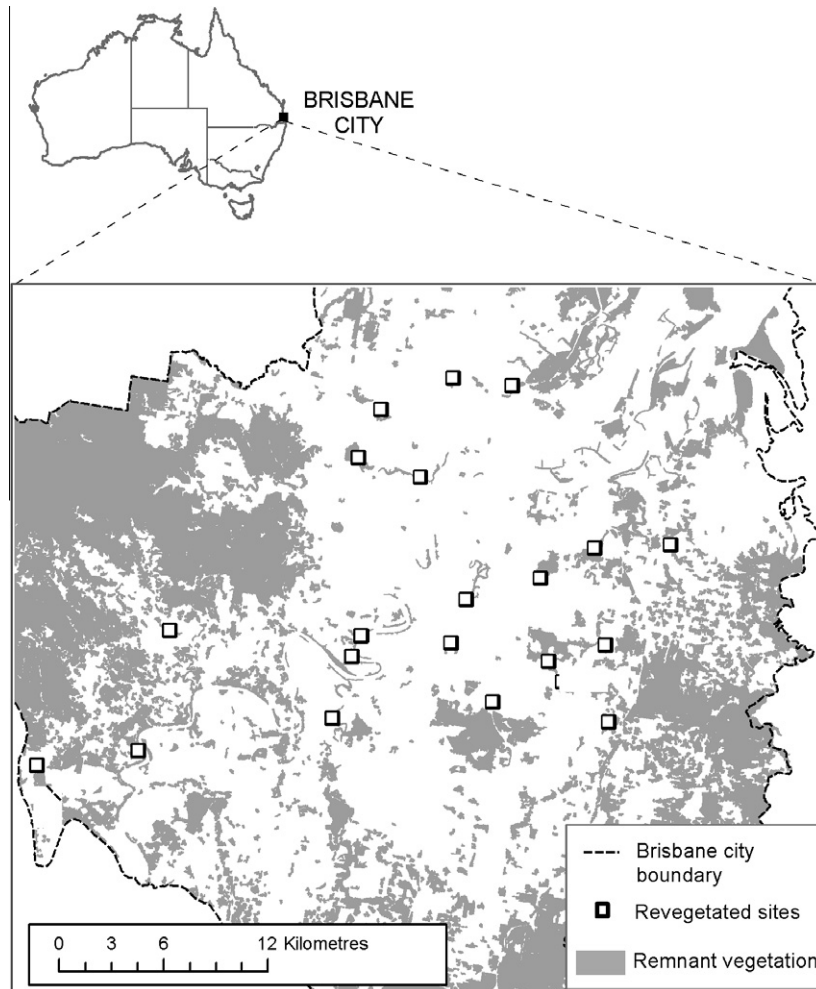


Fig. 1. Map of Brisbane city, with the revegetation sites used in this study shown as white squares. The remnant vegetation in the city and surrounds is shaded (vegetation data are derived from the Regional Ecosystem Mapping V1.0; Brisbane City Council (2004)).

Table 1

Description of bird foraging guilds. Species specific information is derived from the Handbook of Australian, New Zealand and Antarctic Birds (Marchant and Higgins, 1990, 1993; Higgins and Davies, 1996; Higgins, 1999; Higgins and Peter, 2002; Higgins et al., 2006).

Guild	Diet and foraging behaviour	Number of species
Carnivorous	Small mammals, reptiles, amphibians, fish and birds	7
Granivorous	Mostly seeds	7
Herbivorous	Seeds, blossoms, shoots	6
Insectivorous	Predominantly insects, spiders and invertebrates	
Ground	Forages on ground	4
Arboreal/grassy (low vegetation)	Forages in low understory or dense grasses	10
Arboreal (canopy and sub-canopy)	Forages high in tree strata	8
All vegetation levels	Forages at all levels	5
Aerial	Gleans primarily insects from the air	6
Nectarivorous/frugivorous	Plant nectar, fruits, often also insects and spiders	14
Omnivorous	Commonly takes both plant and animal food items	14
		Total: 81

between sites based on the full set of vegetation variables (Minchin, 1987) using the package Ecodist (Goslee and Urban, 2007). We used a graphical method for factor analysis (Cattell Scree test; Cattell, 1966) in the nFactors package (Raiche, 2007) to determine the number of factors that could reasonably describe the majority of the variation in the vegetation data set. Eigenvalues tapered off at two dimensions which explained the vast majority of the variation in the vegetation data. The coordinates resulting from the factor analysis constituted vegetation summary variables in

lieu of the nine original vegetation variables in further analysis, and can be considered approximations of vegetation complexity. The resulting variables are referred to as 'Vege complexity 1' and 'Vege complexity 2'.

2.2.2. Urbanisation

To account for variation in bird species richness and abundance owing to gross variation in urban density, we incorporated human population density (termed 'population density') as a covariate in

our analysis by calculating the number of people resident within a 1 km buffer around the edges of each vegetated patch using the 'Usual Resident Population' estimate from the 2006 census (Australian Bureau of Statistics, 2006).

2.2.3. Patch area and revegetated area

To estimate the area of the revegetation itself ('Revege area') and the total patch area ('Patch area', the area of all vegetation attached to the revegetation with no gaps, inclusive of the revegetation itself), we manually digitised the edges of the vegetation patch and the revegetation using a combination of high resolution imagery obtained from Google Earth (Spot image, captured April 16, 2007) and Landsat imagery (1 km resolution, captured May 19, 2006). We tested the accuracy of these polygons against field GPS data within a GIS environment (ArcGIS 9.2, ESRI, California, USA), as well as against a high resolution vegetation map created by local government environmental authorities (maps all vegetation patches above 0.5 ha, Regional Ecosystems V1.0; Brisbane City Council, 2004). This vegetation map was originally created by local government using satellite imagery and aerial photograph interpretation, and was later ground-truthed and classified.

2.2.4. Connectivity

We measured connectivity of the revegetated patches using a multi-scale graph-theoretical approach, similar to that used by Martensen et al. (2008). This method allowed us to define and link vegetation patches that are potentially functionally connected through different dispersal abilities of species (some species are likely to be able to cross larger areas of cleared land than others). These connectivity measures were the total vegetated (forested) area connected to the revegetated patches with different maximum distances of cleared land: 10 m, 20 m, 30 m, 40 m and 50 m (referred to as, for example, 'connectivity 10 m'). These measurements excluded the patch area measurement described above. We used 50 m as the maximum distance, as beyond this most vegetation patches became connected and hence the value was similar for all revegetated plots.

2.3. Data analyses

We checked for spatial autocorrelation in species richness and abundance at the revegetated sites using a Mantel test (Mantel, 1967). This approach assesses the correlation between two matrices; in this case the first matrix was the geographic distance between revegetated site pairs, and the second matrix was the Sorensen similarity index (Sørensen, 1948) between site pairs, calculated for each of the variables species richness and bird abundance (i.e. two Mantel tests were carried out).

Multivariate regression model selection alone does not allow the user to assess the independent contribution of each variable as these may be masked by the effect of variable combinations, and multicollinearity may generate spurious results (Mac Nally, 1996). As there is likely to be a high level of co-linearity particularly among the connectivity variables used within our study, we used hierarchical partitioning alongside a model selection procedure to identify the connectivity or area variables with most influence on bird species richness and abundance (Chevan and Sutherland, 1991; Mac Nally, 1996, 2000). Hierarchical partitioning is a useful method for identifying the variables to use in subsequent model selection procedures; we used it to identify whether time since planting, vegetation complexity measures, human population density and total revegetated area explained a significant amount of variance in bird abundance and species richness, and thus whether they were confounding the detection of area and connectivity effects. Agreement as to the best predictor variables from both the hierarchical partitioning and model selection

methods indicates there is a strong likelihood that those variables have an important influence over the dependent variable (Mac Nally, 1996). These procedures are described in greater detail below. Both the model selection and hierarchical partitioning procedures were carried out using a Poisson error distribution, as most abundance and species richness values were non-negative low values. For analyses using linear models all area measurements were transformed ($\log + 1$) to satisfy the assumption of linearity between the connectivity area measures and the response variables.

2.3.1. Hierarchical partitioning

Hierarchical partitioning is a statistical method in which all possible combinations of variables are assessed to determine the independent contribution of each variable to model fit (Chevan and Sutherland, 1991). We carried out this analysis using the package hier.part (Walsh and Mac Nally, 2008) in R Version 2.2 (R Development Core Team, 2005), and we used r^2 as the goodness-of-fit measure. We carried out a randomisation procedure to determine the significance for each variable (Mac Nally, 2002), where the data matrix was randomised 1000 times, and the distribution of the explanatory values (I) was calculated. If the observed I value fell above the 95th percentile, we considered it significant. The results of this significance test are expressed as Z-scores, and significance is defined as the upper 95% confidence limit of the normal distribution of Z-scores ($Z \geq 1.65$). This hierarchical partitioning procedure was carried out for each of the response variables species richness, bird abundance, and also bird abundance within each foraging guild. We did not carry out any analysis for species richness within foraging guilds as there was insufficient species numbers for the number of possible explanatory variables (Table 1).

2.3.2. Model selection framework

After determining whether the other variables tested would confound our results, we formulated 16 possible models using only patch area and connectivity variables to explain variation in species richness and abundance (Table 2). These models were created from all possible combinations of the connectivity and patch area variables (though considering only one connectivity variable in each to avoid co-linearity problems), as well as all combinations including an interaction term, to address our main question of their relative importance. We calculated the small sample size adjustment of Akaike's Information Criterion for each model (AICc; Akaike, 1979; Hurvich and Tsai, 1989) using the GLM package in R Version 2.2. For each of the possible 16 models we also calculated $\Delta AICc$ (the difference in AICc between each model and the model with the smallest AICc) and the model likelihood value (AIC weight; wAIC) to rank the models in order from best fit to worst fit. This model selection procedure was carried out for the overall species richness and bird abundance data.

3. Results

3.1. Tests for spatial autocorrelation

Mantel tests indicated that spatial autocorrelation across sites was weak for both the species richness and bird abundance data, with a low, non-significant ($P > 0.05$) correlation coefficient between geographic distance and the mean bird abundance and species richness difference matrices ($r = 0.16$; $r = 0.23$ respectively).

3.2. Influence of variables on species richness and bird abundance

Models including all variables within the hierarchical partitioning procedure were significant for both total species richness and

Table 2

Rankings of the 16 models tested for their influence on bird species richness and abundance in urban revegetation, determined from likelihood measures with a Poisson error distribution. The connectivity variables refer the total vegetated area connected by maximum cleared gaps of the distance noted (10 m, 20 m, 30 m, 40 m, 50 m).

Model	Rank	AICc	Δ AICc	wAIC
<i>Dependent variable: bird species richness</i>				
Connectivity 50 m	1	125.37	0.00	0.21
Connectivity 20 m	2	126.31	0.94	0.13
Connectivity 10 m	3	126.34	0.97	0.13
Connectivity 40 m	4	126.41	1.04	0.12
Patch area	5	126.81	1.44	0.10
Connectivity 30 m	6	127.11	1.74	0.09
Patch area + connectivity 50 m	7	127.90	2.50	0.06
Patch area + connectivity 10 m	8	128.40	3.03	0.05
Patch area + connectivity 20 m	9	128.40	3.03	0.05
Patch area + connectivity 40 m	10	128.70	3.33	0.04
Patch area + connectivity 30 m	11	129.00	3.63	0.03
Patch area + connectivity 50 m + interaction	12	131.13	5.77	0.01
Patch area + connectivity 20 m + interaction	13	131.14	5.78	0.01
Patch area + connectivity 10 m + interaction	14	131.34	5.98	0.00
Patch area + connectivity 40 m + interaction	15	132.22	6.86	0.00
Patch area + connectivity 30 m + interaction	16	132.91	7.55	0.00
<i>Dependent variable: bird abundance</i>				
Patch area + connectivity 30 m	1	207.60	0.00	0.89
Patch area	2	213.51	5.91	0.05
Patch area + connectivity 20 m	3	215.30	7.70	0.02
Patch area + connectivity 10 m	4	215.40	7.80	0.02
Patch area + connectivity 50 m	5	216.00	8.40	0.01
Patch area + connectivity 40 m	6	216.30	8.70	0.01
Patch area + connectivity 40 m + interaction	7	228.11	20.51	0.00
Patch area + connectivity 50 m + interaction	8	230.32	22.72	0.00
Patch area + connectivity 20 m + interaction	9	239.78	32.18	0.00
Patch area + connectivity 30 m + interaction	10	239.99	32.39	0.00
Patch area + connectivity 10 m + interaction	11	241.70	34.10	0.00
Connectivity 40 m	12	267.71	60.11	0.00
Connectivity 50 m	13	271.71	64.11	0.00
Connectivity 20 m	14	279.51	71.91	0.00
Connectivity 10 m	15	279.61	72.01	0.00
Connectivity 30 m	16	280.91	73.31	0.00

total bird abundance ($r^2 = 0.60$, $P = 0.05$ and $r^2 = 0.97$, $P < 0.0001$ respectively).

Hierarchical partitioning revealed that revegetated area, human population density, time since planting and vegetation complexity all had little independent contribution to the variance explained by the full model for both total species richness and bird abundance (Fig. 2a and b), indicating they are unlikely to be confounding factors in our analyses of connectivity and patch area.

For total species richness, of all variables considered in the full model within hierarchical partitioning, connectivity 50 m (i.e. the vegetated area connected by ≤ 50 m of cleared land) had the greatest independent contribution to model fit (Fig. 2a). The model selection procedure supported this result; the model containing only connectivity 50 m ranked highest (Table 2). These results indicate that of the variables considered, connectivity provided the best explanation for the richness of species within revegetated patches, particularly where the gaps between vegetated areas are no more than 50 m.

For total bird abundance, patch area was the only variable of those considered in hierarchical partitioning that independently

contributed significantly to total explained variance (Fig. 2b). However, the model providing best fit to the data based on AICc weight included both the patch area and connectivity 30 m variables (Table 2) (though the interaction term between these variables was not statistically significant and the model including the interaction term ranked much lower; Table 2). The single predictor model containing patch area alone ranked second, indicating that though patch area had the highest independent contribution to bird abundance, the combined effect of the two variables provided the most parsimonious model fit.

For all species foraging guilds, the full model used in hierarchical partitioning achieved r^2 values of between 0.34 and 0.63 for the bird abundance response variable (Table 3). Table 3 summarises the independent contribution of the variables to model fit for each of the bird foraging guilds.

4. Discussion

4.1. Importance of connectivity and patch area for colonisation by birds

In this study landscape connectivity had a greater influence than patch area on bird species richness within urban revegetation, while patch area in combination with connectivity was important for enhanced bird abundance. An explanation for this result is that connectivity increases the number of habitat patches (and total vegetation area) from which colonists can arrive; in fact, for some mobile species increased connectivity is likely to increase effective patch area. In contrast, revegetation that increases patch area expands the habitat available to species already present in a patch and does not necessarily encourage new colonists. These results highlight that when planning revegetation programs in urban landscapes the goal of the program must be clearly defined: is the goal to maximise species richness or maximise population persistence over time? To maximise species richness in the short-term, using revegetation to reduce the gaps that potential colonists must cross may be the most effective approach (i.e. enhancing connectivity). However, this may not help meet long-term conservation objectives as a combined approach is likely to be needed to stabilise populations and allow long-term dispersal processes to re-establish or continue. For example, Stouffer and Bierregaard (2007) found that enhancing connectivity allowed bird communities to establish and approach pre-clearing numbers only in larger habitat remnants. Enhancing patch size may also provide further benefits that enhance long-term survival of populations through reducing the level of predator invasion and habitat degradation; these threats can be particularly significant in small urban remnant vegetation patches (e.g. Rose and Fairweather, 1997; Piper and Catterall, 2006).

The level of connectivity that appeared to have greatest influence on species richness in this study was at a scale of 50 m gaps between vegetation remnants. This provides an indication of the minimum level at which connectivity objectives should be set in this particular urban environment; this kind of information has repeatedly been identified as crucial for effective practical landscape planning (Bowman and Fahrig, 2002; With and King, 1999).

Our results show that different characteristics of revegetation influence the abundance of birds within foraging guilds differentially. This result is important because different conservation programs might focus on different foraging guilds, perhaps because of variation in their conservation status. For example, insectivores often show markedly reduced abundance in urban environments, while frugivores can increase if they benefit from street tree plantings (DeGraaf and Wentworth, 1986; Lim and Sodhi, 2004). In our study patch area was particularly important for carnivorous

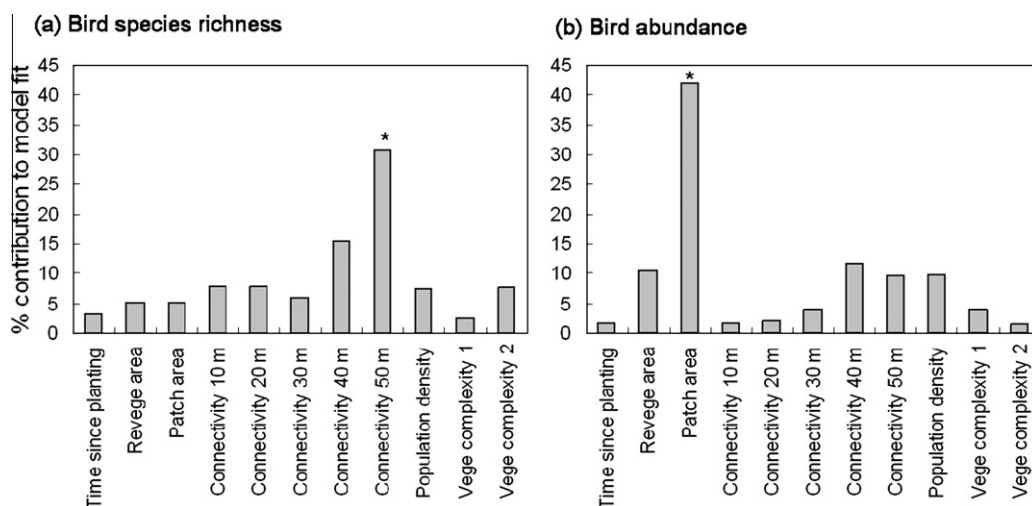


Fig. 2. The independent contribution of each variable to model fit for (a) bird species richness and (b) bird abundance data, as determined by hierarchical partitioning. The model includes all variables indicated in the figure. An asterisk indicates the variables for which the proportion of independent contribution to overall model fit was significant at $P \leq 0.05$. Species richness is the total number of bird species seen across all surveys, bird abundance is the mean number of individuals recorded. See text for descriptions of variables.

Table 3

The independent contribution of each variable to model fit (where the model incorporated all variables indicated in the table) for bird abundance of each species feeding guild (results from hierarchical partitioning). Also presented is the overall r^2 and significance value for the complete model for each species group. Statistically significant variables at $P \leq 0.05$ are indicated by an asterisk. These significant variables are italicized for emphasis, as are the variables which explain the highest proportion of variance for guilds where none is statistically significant. The labels 'Con 10–50' refer to the variable 'connectivity', measured as the total vegetated (forested) area connected to the revegetated patches with different maximum distances of cleared land: 10 m, 20 m, 30 m, 40 m and 50 m.

Feeding guild	Percentage of variance explained by the variable											Model r^2 value (and significance)
	Time since planting	Revege area	Patch area	Con 10	Con 20	Con 30	Con 40	Con 50	Population density	Vege complexity 1	Vege complexity 2	
<i>Bird abundance within guild</i>												
<i>Carnivorous</i>	0.5	24.1	25.9*	3.7	5.2	3.9	6.5	6.8	16.7	3.8	2.9	0.63 (0.11)
<i>Granivorous</i>	1.2	8.6	1.4	5.3	3.1	1.9	15.4	22.9*	4.3	15.2	20.6	0.52 (0.31)
<i>Herbivorous</i>	9.1	8.4	10.7	2.7	4.2	10.8	4.6	4.0	8.3	15.5*	21.6*	0.34 (0.74)
<i>Insectivorous</i>												
Ground	1.2	1.6	23.5*	7.6	5.1	3.4	15.9	11.7	2.8	19.5	7.6	0.51 (0.05)
Arboreal/grassy (low vegetation)	2.5	14.6	29.1*	9.9	6.2	5.7	4.4	5.5	7.2	4.2	10.7	0.47 (0.42)
Arboreal (canopy and sub-canopy)	3.5	1.4	19.8	15.7	8.1	7.5	11.8	10.6	10.1	0.8	10.7	0.63 (0.63)
All vegetation levels	3.3	3.7	26.7*	3.8	2.8	1.4	4.2	5.6	11.1	35.3*	2.0	0.56 (0.23)
<i>Aerial</i>	0.3	2.4	10.8	16.1	12.5	8.3	17.8	14.2	12.2	0.9	4.4	0.48 (0.45)
<i>Nectarivorous/frugivorous</i>	6.5	3.9	4.6	7.6	6.2	8.0	10.8	12.5	2.6	31.3*	6.0	0.57 (0.21)
<i>Omnivorous</i>	0.1	1.0	8.7	6.5	5.6	5.3	26.5	27.5*	10.4	5.2	3.1	0.41 (0.48)

species and all insectivorous guilds, indicating that these species groups may require substantial habitat extent connected by little or no gaps in vegetation. Though it seems unlikely that gaps as little as 10 m should present such an effective barrier to birds, even small roads have been found to effectively create territory boundaries, and as such inhibit crossing behaviour (Develey and Stouffer, 2001). Our results are consistent with previous research that shows low foraging insectivorous birds are particularly susceptible to both patch area decline and disruptions in connectivity (e.g. Martensen et al., 2008; Willis and Murphy, 1979). Barrett et al. (2007) showed that restoration of native shrub and grass species within revegetated sites helped recover populations of ground-foraging insectivores.

Bird species richness has repeatedly been found to increase with vegetation complexity (Castillo-Guerrero et al., 2009; Evans et al., 2009; Huste et al., 2006). Within revegetated areas, more mature plantings generally have improved vegetation complexity and provide more diverse habitats (Vesk et al., 2008). Contrary to this generalisation, we found no effect of time since planting

on bird species richness and abundance. A possible explanation for this result is that the revegetated patches in our study were too young to display much variation in vegetation complexity (all patches <25 years old). Second, the structural complexity of the patches may be homogenised through disturbance associated with urban environments and recreational use, as well as continued weeding which is carried out to maintain the integrity of the plantings. We did however find that vegetation characteristics were important in determining abundance within some feeding guilds. Region specific research into the vegetation management and planting strategies that encourage rapid development of vegetation complexity could potentially improve bird biodiversity gains from urban revegetation projects.

4.2. Revegetation as a conservation strategy in urban landscapes

From a conservation viewpoint, urban green spaces cannot be judged on the same criteria as natural areas given the wide range of human values associated with them (McDonnell, 2007). Urban

parklands often represent one of the few opportunities city residents have to encounter nature on a daily basis (McDonnell, 2007), and this is particularly important as over half of the world's human population now live in urban areas (United Nations, 2008). Further to this, recent evidence shows that the psychological benefits of urban green space increase with species richness (Fuller et al., 2007). This suggests that the provision of urban green space with the goal of maximising bird species richness could be important whether or not it is contributing to regional and national conservation goals. Given that long-term persistence of bird species in a local patch can require upward of 100 territories of connected habitat (Jones and Diamond, 1976; Shanahan and Possingham, 2009), we recognise that in many urban landscapes it is probably impossible to restore and protect sufficient habitat for species which require unbroken tracts of vegetation. This said, populations of some species of conservation concern can be supported in urban environments (Fuller et al., 2009) so these decisions need to be made on a case-by-case basis.

Urban revegetation is likely to provide multiple benefits to a range of taxa, and is frequently used by local governments to achieve multiple public service objectives. It can contribute to decreasing the heat island effect in high density cities (e.g. Tokyo, Japan; Tetsuya et al., 2001), reducing soil erosion and improving water quality (e.g. Chesapeake Bay watershed; Sutton et al., 2010), and can also 'make the city greener' (e.g. Brisbane, Australia; Brisbane City Council, 2009). Any revegetation project will therefore require a multi-objective planning approach to ensure all identified goals are met (Maron and Cockfield, 2008; Vesk and Mac Nally, 2006). However, we have shown that where one objective is to enhance bird biodiversity, promoting connectivity and reducing the gaps between existing vegetation may achieve this locally and in the short-term. For long-term persistence of species, increasing the total available habitat area (and for some species this needs to be considered as area with no discernable gaps) may be the best strategy.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.10.014.

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