

Perspective

Effects of Landscape Pattern on Bird Species Distribution in the Mt. Lofty Ranges, South Australia

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Abstract

We assessed how well landscape metrics at 2, 5, and 10 km scales could explain the distribution of woodland bird species in the Mount Lofty Ranges, South Australia. We considered 31 species that have isolated or partially isolated populations in the region and used the Akaike Information Criterion to select a set of candidate logistic regression models. The 2 km distance was the most appropriate scale for a plurality of the species. While the total amount of area of native vegetation around a site was the most important determining factor, the effect of landscape configuration was also important for many species. Most species responded positively to area-independent fragmentation, but the responses to mean patch isolation and mean patch shape were more variable. Considering a set of candidate models for which there is reasonable support (Akaike weights > 0.10), 12 species responded negatively to landscapes with highly linear and isolated patches. No clear patterns emerged in terms of taxonomy or functional group as to how species respond to landscape configuration. Most of the species had models with relatively good discrimination (12 species had ROC values > 0.70), indicating that landscape pattern alone can explain their distributions reasonably well. For six species there were no models that had strong weight of evidence, based on the AIC and ROC criteria. This analysis shows the utility of the Akaike Information Criterion approach to model selection in landscape ecology. Our results indicate that landscape planners in the Mount Lofty Ranges must consider the spatial configuration of vegetation.

Keywords: Akaike information criterion; Australian birds; fragmentation; landscape metrics; logistic regression; receiver operating characteristic

Introduction

With the advent of the landscape paradigm in ecology, there has been great attention paid to how landscape configuration affects species distribution and population dynamics (Turner et al. 2001). However, the impacts of the fraction of suitable habitat in the landscape as opposed to landscape configuration, which includes such properties of landscape pattern as patch shape, isolation and fragmentation, are often difficult to disentangle, and this has important implications for how we manage habitat loss and/or reconstruction. In a simulation study Fahrig (1997, 1998) found that when the percentage of habitat in a landscape exceeds 20%, then species persistence was virtually assured, regardless of the spatial configuration of the habitat. A review of birds and mammals by Andren (1994) also suggests that habitat patch isolation only becomes important in terms of species richness or abundance when the percentage of habitat decreases below a 20–30% threshold.

Empirical studies of birds, for instance, vary widely in terms of the importance of the spatial pattern of habitat even when they have analyzed landscapes with large ranges of percent habitat cover. McGarigal and McComb (1995) found in a study of birds in Oregon that forest cover explained more variance in species abundance than landscape structure, and most of the significant effects of fragmentation on abundance were positive. Meyer and Irwin (1998) found that the main influences of landscape structure on spotted owls were due to the amount of habitat, not configuration. Trzcinski et al. (1999) compared the effects of forest cover and area-independent fragmentation (using the residuals of the correlation between habitat area and a measure of fragmentation) on breeding bird distributions of 31 species in forested landscapes in Ontario. They found that all species responded positively to

forest cover, while the response to fragmentation was weak and variable. However, in another study in eastern Ontario with similar forest types and range of percent cover, Villard et al. (1999) determined that more than half of the species had measures of landscape configuration as significant explanatory variables in models of species occupancy. Unlike Trzcinski et al. (1999), they used a smaller landscape scale and included a measure of patch isolation. Even within a species the effect of fragmentation has been shown to vary across regions with different proportions of habitat cover. The Scarlet Tanager showed its strongest response to fragmentation in the more deforested Midwest and Atlantic regions of its range in North America (Rosenberg et al. 1999). Fahrig (2002) asserts that fragmentation effects are as likely to be positive as negative based on the limited empirical studies to date. Indeed, there is a discordance between the predictions of models and the rather equivocal results of empirical studies.

The main goal of this study was to look at how well landscape variables measured at various spatial scales (2, 5, 10 km) explain the distribution of wood-land bird species in the Mount Lofty Ranges (MLR) region of South Australia. At the time of World War II, about half of the region was covered by native vegetation, and since then, there has been precipitous clearing for agriculture, particularly in the southern part of the peninsula (Bryan 2000). Garnett and Crowley (2000) list eight species that have already gone extinct in the MLR. Because of the relatively recent land clearance, there may exist an *extinction debt*, with more species doomed before a relaxation to a new level of species richness (Possingham and Field 2001). In order to develop plans for habitat reconstruction in the region, it is necessary to understand the landscape determinants of species distributions.

Unlike previous studies, we have used the techniques of Akaike Information Criterion (AIC) and the Receiving Operator Characteristic (ROC) for model selection and discrimination, respectively. Because of the large spatial scale over which the bird survey data were collected, the analysis was not amenable to the inclusion of patch-level variables; that is, the survey data were from searched areas larger than one patch. Our first goal was to determine if they landscape variables alone could explain the species distributions adequately. Secondly, we sought to determine the relative importance of area measures versus landscape configuration variables in determining the species occupancy.

Methods

Study site

The Mount Lofty Ranges (MLR) of South Australia is a relatively high rainfall (400 mm/yr–1100 mm/yr) region, amidst semi-arid land (Figure 1). Of a total 500,000 ha, only about 10–18% is covered by native vegetation with an understory, primarily eucalypt woodland (particularly *Eucalyptus baxteri*, *Eucalyptus fasciculosa*, *Eucalyptus leucoxylon*, *Eucalyptus obliqua*, *Eucalyptus riminalis*) in a matrix of mixed agricultural land, including pasture, cropland, vine-yards, and orchards (Bryan 2000). There are a total of about 4,000 native woodland patches (mean = 13.1 ha, standard deviation of 26.5 ha) in the MLR. The region is a ‘biological island’, and using atlas data, we have defined 37 woodland bird species as having populations that are isolated or partially isolated from their nearest populations outside the MLR (Paton et al. 1994).

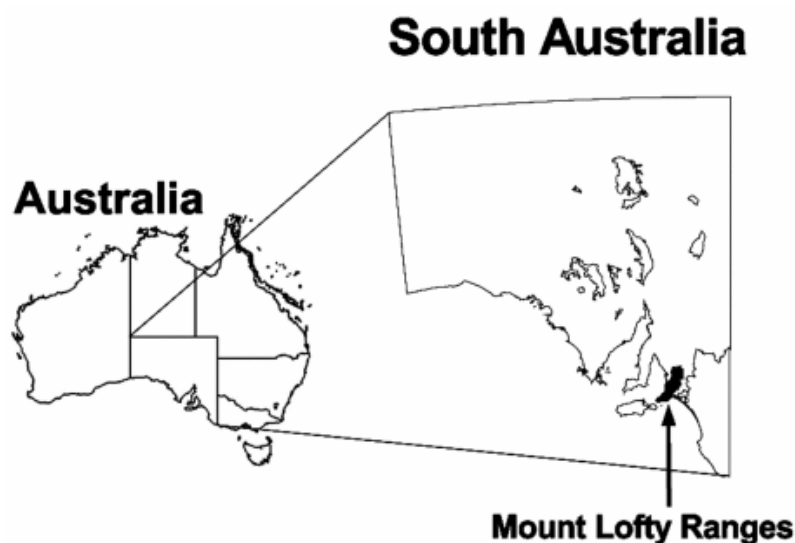


Fig 1. The study site in Australia

Bird distribution data

In 1984–85, the South Australian Ornithological Association conducted an intensive survey of birds in Adelaide region of South Australia, including the MLR (Paton et al. 1994). The basic survey method involved overlaying the region with a grid having squares of 10,000 yrd × 10,000 yrd, in agreement with a previous Royal Australasian Ornithologists Union atlas undertaken in 1974–75, and surveying at least one point in each grid cell. In all, the Adelaide region bird atlas included of 268 grid squares, over 1700 survey points, 6000 individual surveys, and 100,000 observations. In some cases, the survey points noted represented a center point of perhaps an area of 5–6 km × 5–6 km that was searched, and in other cases, they reflect a much more localized area. Though variation was evident in the number of surveys per point and in the effective survey area for each point, there is assumed to be no systematic variation across the region. The accuracy of the coordinates is probably within 1–2 minutes of latitude and longitude (D. Paton, pers. comm.). The observers re-corded all species that were seen or heard during the census. Using the boundaries of the MLR as defined hydrolgically by Bryan (2000), we selected only those survey points having native vegetation within a distance of 2 km in order to keep the sample size constant among all models at the three scales. There are 499 survey points for the MLR region (Figure 2). We considered a species present at a survey point if it was recorded there during at least one survey over the two years of the bird atlas study. We employed a Geographic Information System (GIS) of the vegetation in the region, which was compiled by the South Australia Department of Environment and Heritage in 1986 using aerial photographs and ground surveys.

Mount Lofty Ranges

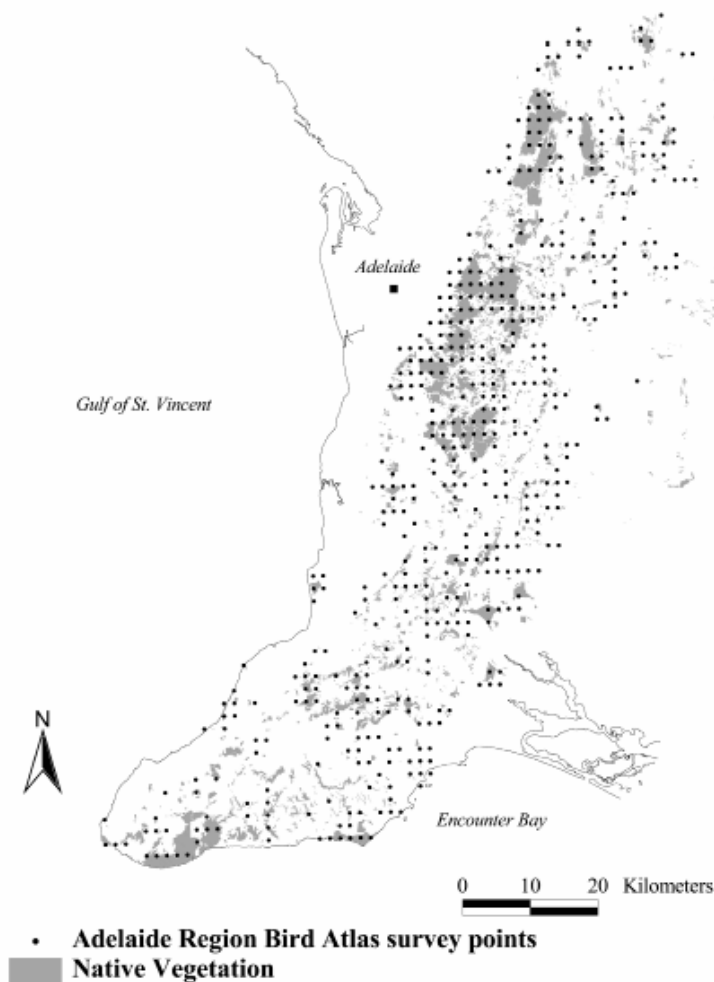


Fig. 2. The Mount Lofty Ranges native vegetation and location of bird atlas survey points.

Landscape metrics

We created buffered areas with radii of 2, 5, and 10 km around each survey point and intersected those areas with the native vegetation coverage, using the Avenue scripting language in ArcView 3.2a (ESRI Inc. 2000). That is, we selected "minilandscapes" around each survey point at various scales for later characterization with the landscape metrics. We considered a binary landscape (either native vegetation or not) and did not more finely delineate the various native vegetation types. We used Patch Analyst, an extension in ArcView 3.x (Elkie et al. 1999), to calculate some standard FRAGSTATS metrics (McGarigal and McComb 1995) for the buffered areas around each point: total landscape area of native vegetation (TLA), mean perimeter area ratio of patches (MPAR), mean nearest neighbor distance (edge to edge) of patches (MNN), and landscape shape index (LSI), which is a measure of the total native vegetation-matrix edge in the landscape. LSI is the amount of edge in the landscape divided by the square root of area and adjusted for the vector form of the coverage. It equals 1.0 when the landscape consists of just one circular patch. It increases without bound as the landscape shape becomes more irregular or as the number of patches increases (McGarigal and McComb 1995). The scale of the survey area was larger than a single patch, so we ignored the patch-specific measures and included only the landscape metrics, which are measures of mean values in the buffered landscapes. We did not have much confidence in the mapping of broad vegetation community classes, and we did not have data on fine-scale vegetation features that may be important (e.g., vegetation structure, nectar sources, disturbance history, amount of non-native weeds, etc.) (Neave et al. 1996). Over this spatial scale, climatic variables would probably be poor explanatory variables. In a study in open eucalypt forest in southeastern Australia over a much larger spatial scale, Neave et al. (1996) found that out of seven species modeled, only one species had distribution best explained by climatic variables.

In order to remove correlations between the metrics, we performed simple linear regression (S-Plus 4.5, MathSoft Inc., 1998) (Trzcinski et al. 1999). Though LSI is adjusted for the total landscape area, we nonetheless regressed it by TLA and used the residuals as the adjusted measure of LSI (fragmentation). We then regressed MPAR and MNN separately by TLA and the adjusted LSI and used the residuals as adjusted measures of MPAR and MNN. We also tried regressing instead MAPR by the three other variables and taking the residuals as a measure of MPAR (and such removing the tiny correlation between MPAR and MNN $r < 0.4$ for all three distance classes), but this did not qualitatively change the results. Thus, our four explanatory variables (TLA, LSI, MPAR, MNN) are completely uncorrelated with each other.

Logistic Regression Models and AIC

We used the landscape metrics as explanatory variables in logistic regression analyses of bird species occupancy for the survey points in the MLR. We considered only species that are isolated or partially isolated in the MLR (based on Paton et al. (1994) and expert opinion of HP as to whether there is significant dispersal between the populations within and outside the MLR) and present in at least 5% of the sites. This gives a total of 31 species (Table 1). Some other species with isolated or partially isolated populations, such as the Beautiful Firetail (*Stagonopleura bella*), Chestnut-rumped Hylacola (*Sericornis pyrrhopygii*), Tawny-crowned Honeyeater (*Phylidonyris melanops*), Black-chinned Honeyeater (*Melithreptus gularis*), Bassian thrush (*Zoothera lunulata*), and Diamond Firetail (*Stagonopleura guttata*) were simply recorded at too few points. Though a model with so few presences may actually discriminate well between species presences and absences, the small data set may not be representative of the species as a whole.

We evaluated all possible combinations of the four explanatory variables in the logistic regression, modeling the three distance scales separately. This gives a total of 45 models for each species (15 models for each distance scale). We did not consider interactions among the variables. We fitted the generalized linear models (GLM) using S-Plus 4.5 (MathSoft Inc., 1998).

We evaluated the spatial autocorrelation of both the independent and dependent variables with Mantel tests (Fortin and Gurevitch 1993; Legendre 1993; Koenig and Knops 1998; Koenig 1999). Mantel tests evaluate the similarity between a matrix of ecological distance (1 - similarity in some ecological variable) and the matrix of geometric distance. If spatial auto-correlation exists, then the closer points are in geometric space, the more similar should the values be of some ecological variable. The ecological distance for the response variable (species presence and absence) was calculated using the Jaccard similarity index, which measures the similarity in species assemblages among survey sites (Legendre and Legendre 1983). Likewise, for all the independent variables (the landscape metrics) combined, we calculated the Gower similarity index between all pairs of sites (Legendre and Legendre 1983). In both cases, we found spatial autocorrelation, which is not surprising, given that the

neighborhoods around nearby survey points overlap in some cases. In the original bird atlas, the extent of this has not been documented very well. This is an often intractable problem when historical data are appropriated for a later uses. However, spatial autocorrelation does not affect the relative influence of the explanatory variables (Trzcinski et al. 1999). In this case, spatial autocorrelation simply inflates the sample size. Here we are not using traditional significance tests of the Fisherian/inferential statistics paradigm to evaluate models, but AIC values, which do not depend on sample size. Since the survey points are rather evenly distributed across the landscape, the spatial autocorrelation does not bias the contribution of certain survey points. If some of the survey points were clumped, then spatial autocorrelation would be problematic, and the weightings of those points would have to be altered in the regression.

We employed the Akaike Information Criterion (AIC) to select the best models. The AIC has its roots in Kullback-Leibler (KL) information and statistical maximum likelihood (Burnham and Anderson 1998; Anderson et al. 2000; Burnham and Anderson 2001).

Table 1. Isolated or partially isolated bird species in the Mount Lofty Ranges with presences \geq 5% of survey points.

Species	Presences (out of 499)
Striated Thornbill, <i>Acanthiza lineata</i>	250
Brown Thornbill, <i>Acanthiza pusilla</i>	151
Buff-rumped Thornbill, <i>Acanthiza reguloides</i>	112
Eastern Spinebill, <i>Acanthorhynchus tenuirostris</i>	165
Little Wattlebird, <i>Anthochaera chrysoptera</i>	64
Sulfur-crested Cockatoo, <i>Cacatua galerita</i>	86
Fan-tailed Cuckoo, <i>Cacomantis flabelliformis</i>	119
Yellow-tailed Black-Cockatoo, <i>Calyptorhynchus funereus</i>	130
Shining Bronze-cuckoo, <i>Chrysococcyx lucidus</i>	30
Brown Treecreeper, <i>Climacteris picumnus</i>	27
White-winged Chough, <i>Corcorax melanorhamphos</i>	34
White-throated Treecreeper, <i>Cormobates leucophaeus</i>	200
Laughing Kookaburra, <i>Dacelo novaeguineae</i>	237
Crested Shrike-tit, <i>Falcunculus frontatus</i>	69
Musk Lorikeet, <i>Glossopsitta concinna</i>	101
Yellow-faced Honeyeater, <i>Lichenostomus chrysops</i>	228
Superb Fairy-wren, <i>Malurus cyaneus</i>	183
Whitenaped Honeyeater, <i>Melithreptus lunatus</i>	161
Red-browed Finch, <i>Neochmia temporalis</i>	130
Golden Whistler, <i>Pachycephala pectoralis</i>	199
Spotted Pardalote, <i>Pardalotus punctatus</i>	55
Scarlet Robin, <i>Petroica multicolor</i>	192
Brush Bronzewing, <i>Phaps elegans</i>	25
New Holland Honeyeater, <i>Phylidonyris novaehollandiae</i>	160
Crescent Honeyeater, <i>Phylidonyris pyrrhoptera</i>	207
Adelaide Rosella, <i>Platycercus elegans</i>	215
Eastern Rosella, <i>Platycercus eximius</i>	35
Grey Fantail, <i>Rhipidura fuliginosa</i>	238
White-browed Scrubwren, <i>Sericornis frontalis</i>	135
Grey Currawong, <i>Strepera versicolor</i>	210
Rainbow Lorikeet, <i>Trichoglossus haematodus</i>	158

The value for AIC is,

$$AIC = -2\ln(\ell(\hat{\theta}|data)) + 2k \quad (1)$$

where $\ln(\ell(\hat{\theta}|data))$ is the value of the maximized log-likelihood over the unknown parameters (θ), given the data and the model, and k is the number of model parameters. It is insufficient to simply select the model with the lowest AIC value. Other models may have AIC values very close to that of the best model, and the model selection uncertainty cannot be ignored. The evidence for each

alternative model can be determined by evaluating the difference between model AIC and the minimum AIC,

$$\Delta_i = AIC_i - \min AIC \quad (2)$$

The larger the Δ_i , the smaller the likelihood of that model being the best model in the set of candidate models considered. Models having $\Delta_i < 2$ can be considered as having substantial support as candidate models (Anderson et al. 2000; Burnham and Anderson 2001).

Alternatively, one can use Akaike weights, w_i , as indicators of the strength of evidence for the i model,

$$w_i = \frac{\exp\left(\frac{-\Delta_i}{2}\right)}{\sum_{r=1}^R \exp\left(\frac{-\Delta_r}{2}\right)} \quad (3)$$

The w_i can be interpreted approximately as the probability that model i is the best K-L model in the set of R models being considered (Burnham and Anderson 1998; Anderson et al. 2000; Burnham and Anderson 2001). We determined a set of plausible candidate models for each species by including only those with $w_i > 0.1$, which is comparable to the Δ_i criterion above. Using AIC has many advantages over traditional inferential statistics, most notably its ability to address model selection uncertainty.

Inferential statistics can only compare two models at a time, while AIC methods allow one to simultaneously evaluate a whole suite of candidate models. Like Bayesian statistics, it is rooted in the more intellectually robust and practically relevant idea of multiple working hypotheses, instead of a single null vs. alternative hypothesis. This paradigm of multiple working hypotheses is more easily amenable to the communication with the public and thus is more useful in applied ecology and environmental science. Anderson et al. (2000) give an exegesis of the problems related to p-values and hypothesis testing of traditional inferential statistics, including: the misinterpretation of the meaning of a p-value, the α -level is without theoretical basis, the creation of "strawman" null hypotheses, and the fact that a p-value is explicitly conditional on the null hypothesis and is dependent on the sample size. For logistic regression, traditional likelihood ratio tests can only compare nested models, while AIC does not have this limitation (Burnham and Anderson 1998; Anderson et al. 2000; Burnham and Anderson 2001).

Model validation

There are two different aspects of model validation. Discrimination refers to the ability of the model to distinguish between occupied and unoccupied sites, while calibration describes the agreement between the model predictions and actual observations (Pearce and Ferrier 2000). A model could predict the probabilities well in a relative sense (discrimination) but not in an absolute sense (calibration). Here we are concerned with the ability of the model to differentiate between presences and absences, so we only consider model discrimination.

Traditional measures of model discrimination capacity depend on an arbitrary cutoff for translating the predicted probabilities into presence or absence, often 0.5 (Pearce and Ferrier 2000). The choice of the cutoff depends on whether one wants to minimize the number of false positives or false negatives. For instance, using logistic regression to select reintroduction sites for an endangered species requires a high threshold probability in order to minimize the failure of reintroduction and reduce the number of false positives, the sites erroneously predicted to be suitable habitat. However, using logistic regression to model habitat selection in an area proposed for development requires a low threshold probability to be precautionary about a species occurrence across the landscape and minimize the number of false negatives. Moreover, typical measures of model performance using specificity (proportion of predicted negatives to true negatives) and sensitivity (proportion of predicted positives to true positives) may be misleading if the species occurs at almost all or none of the sites, as the accuracy measure is sensitive to the frequency of the species occurrence in the test sample (Pearce and Ferrier 2000).

One threshold independent discrimination method is the Receiver Operating Characteristic (ROC) curve, which involves plotting each pair of true positive and false positive proportions for every possible decision threshold between 0 and 1 (Fielding 1997; Elith 2000; Pearce and Ferrier 2000). The area under the ROC curve can be roughly interpreted as the probability that a model will correctly distinguish a true presence and a true absence drawn at random (Pearce and Ferrier 2000). A value of

0.5 indicates that the model is no better than random. We computed the ROC value for every candidate model for each species, using the jackknifed original data (S-Plus 4.5, MathSoft Inc., 1998).

Results

Tables 2 and 3 show the results of the logistic regression analyses for 25 species which had models with Akaike weights greater than 0.1 and ROC values greater than 0.60. This latter value is arbitrary and we could apply a more stringent criterion for model discrimination, but our goal is primarily inference as opposed to model development for prediction. Species consistently responded positively to the total area of native vegetation, while the responses to the other configuration measures were quite variable. Based only on the model with the highest Akaike weight for each species, 22 species responded positively to landscape area, while only three responded negatively. If one includes the candidate models for each species with Akaike weights greater than 0.1, then 17 and 8 species responded positively and negatively, respectively, to fragmentation. The converse is true for mean patch shape and mean patch isolation. Considering all candidate models, then 16 and 18 species responded negatively to landscape with highly linear patch shapes and high isolation, respectively, while 9 and 5 responded positively to landscapes with those characteristics. More species responded better to landscape metrics at the 2 km scale than the larger distance scales, as is evidenced by which models have the highest Akaike weights.

The distribution of the Crested Shrike-tit showed no landscape effects, and the best model was derived by fitting simply a random explanatory variable. No models for the Sulphur-crested Cockatoo, Laughing Kookaburra, Little Wattlebird, Rainbow Lorikeet, and Superb Fairy-wren had ROC values greater 0.60, indicating that landscape metrics alone for these species are insufficient to explain their distributions.

Discussion

The results generally concur with the work of McGarigal and McComb (1995) in finding that area is generally more important than landscape configuration. Of the species that had reasonably discriminating models, all but one had landscape area as an explanatory variable in the candidate model with the highest Akaike weight, while the configuration measures (particularly MPAR and MNN) were not always part of the best candidate model (Tables 2 and 3). Only three species responded negatively to the area of native vegetation around survey points: the Musk Lorikeet, Adelaide Rosella and the New Holland Honeyeater. Both make extensive use of matrix habitat. The Musk Lorikeet utilizes fruit orchards in the region, and the Adelaide Rosella and New Holland Honeyeater are common in suburban parks and gar-dens and occur throughout the metropolitan area of Adelaide (Paton et al. 1994).

Most of the species responses positively to area-independent fragmentation. Many of the woodland birds in the MLR are found in small fragments, so this may be indicative of an insensitivity by many species to small patch size and a greater importance on the number of patches in the landscape. Species that responded positively to fragmentation had inconsistent responses to mean patch shape and isolation. The effect of the landscape configurations is a function of the degree of matrix utilization by a species. The type of matrix habitat can mitigate the negative aspects of the configuration of the native vegetation, and our ignoring of the matrix is a limitation of this study. The results illustrate the importance of disentangling the confounding components of what is commonly referred to as fragmentation. The reduction of habitat area often results simultaneously in more irregular shaped patches, greater patch number and higher patch isolation.

Table 2. Results of the logistic regression analyses of bird species distributions^a.

Species	km.	Candidate Models	ΔAIC	w	ROC
Striated Thornbill	2	TLA+LSI-MPAR	0.00	0.45	0.67
	2	TLA+LSI	1.63	0.20	0.67
	2	TLA+LSI+MNN-MPAR	1.79	0.19	0.67
Brown Thornbill	2	TLA+LSI-MNN-MPAR	0.00	0.66	0.67
	2	TLA-MNN-MPAR	2.35	0.20	0.67
Buff-rumped Thornbill	2	TLA	0.00	0.22	0.65
	2	TLA-MPAR	0.31	0.19	0.64
	2	TLA-LSI	1.02	0.13	0.62
Eastern Spinebill	2	TLA-LSI-MPAR	1.37	0.11	0.63
	2	TLA+LSI-MNN-MPAR	0.00	0.48	0.68
	2	TLA+LSI-MPAR	0.29	0.42	0.68
Fan-tailed Cuckoo	5	TLA+MNN	0.00	0.17	0.70
	2	TLA+LSI-MPAR	0.15	0.15	0.72
	2	TLA-MPAR	0.54	0.13	0.73
Y.t. Black-Cockatoo	5	TLA+MNN-MPAR	0.97	0.10	0.70
	5	TLA+LSI	0.00	0.35	0.70
	5	TLA+LSI+MNN	1.46	0.17	0.70
Sh. Bronze-Cuckoo	5	TLA+LSI-MPAR	2.00	0.13	0.69
	5	TLA+LSI	0.00	0.35	0.68
	5	TLA+LSI-MNN	1.88	0.14	0.68
Brown Treecreeper	5	TLA+LSI+MPAR	1.96	0.13	0.67
	2	TLA-LSI	0.00	0.37	0.75
	2	TLA-LSI-MPAR	0.54	0.28	0.74
W.w. Chough	2	TLA-LSI+MNN	2.00	0.14	0.73
	2	TLA-LSI+MNN-MPAR	2.54	0.10	0.73
	5	TLA-MNN-MPAR	0.00	0.25	0.74
W.t. Treecreeper	10	-LSI	0.83	0.16	0.72
	5	TLA+LSI-MPAR	0.00	0.32	0.78
	5	TLA-LSI+MPAR	0.48	0.26	0.78
Musk Lorikeet	2	TLA+LSI-MNN-MPAR	1.36	0.16	0.78
	2	TLA+LSI-MNN-MPAR	1.91	0.13	0.78
	5	-LSI+MPAR	0.00	0.49	0.67
Y.f. Honeyeater	5	-TLA-LSI+MPAR	1.64	0.21	0.66
	5	-LSI+MNN+MPAR	1.71	0.21	0.67
	2	TLA-MNN-MPAR	0.00	0.31	0.71
W.a. Honeyeater	2	TLA-MNN	1.13	0.17	0.71
	2	TLA+LSI-MNN-MPAR	1.55	0.14	0.70
	10	TLA+LSI	0.00	0.19	0.68
Red-browed Finch	10	TLA	0.49	0.14	0.68
	10	TLA+LSI-MNN	1.10	0.11	0.68
	5	TLA+MNN	0.00	0.41	0.62
Golden Whistler	5	TLA+MNN+MPAR	1.71	0.18	0.61
	5	TLA-LSI+MNN	1.98	0.15	0.61
	2	TLA+LSI-MPAR	0.00	0.66	0.71
	2	TLA+LSI-MNN-MPAR	1.99	0.24	0.71

Table 2. Continued.

Species	km.	Candidate Models	Δ AIC	w	ROC
Spotted Pardalote	10	TLA-LSI	0.00	0.19	0.72
	5	TLA-LSI	0.30	0.16	0.72
	10	TLA-LSI-MNN	0.32	0.16	0.71
	10	TLA-LSI-MPAR	0.50	0.15	0.71
	10	TLA-LSI-MNN-MPAR	0.81	0.13	0.70
Scarlet Robin	2	TLA+LSI-MPAR	0.00	0.62	0.76
	2	TLA+LSI-MNN-MPAR	1.53	0.29	0.75
Brush Bronzewing	2	TLA-LSI-MNN-MPAR	0.00	0.44	0.79
	2	TLA-LSI-MPAR	0.95	0.27	0.79
	2	TLA-MNN-MPAR	1.73	0.18	0.76
N.h. Honeyeater	10	-TLA+LSI	0.00	0.31	0.60
	10	-TLA+LSI+MNN	1.21	0.17	0.61
	10	-TLA	1.26	0.16	0.60
Crescent Honeyeater	2	TLA+LSI-MPAR	0.00	0.56	0.77
	2	TLA+LSI-MNN-MPAR	0.62	0.41	0.77
Adelaide Rosella	10	-TLA+LSI-MPAR	0.00	0.48	0.64
	10	-TLA+LSI+MNN-MPAR	1.40	0.24	0.64
	10	-TLA+LSI	1.95	0.18	0.63
Eastern Rosella	10	TLA-MNN+MPAR	0.00	0.26	0.72
	10	TLA-MNN	0.25	0.23	0.72
	10	TLA-LSI-MNN+MPAR	1.27	0.14	0.69
	10	TLA-LSI-MNN	1.61	0.12	0.68
Grey Fantail	10	TLA+LSI	0.00	0.46	0.70
	10	TLA+LSI+MNN	1.12	0.27	0.70
	10	TLA+LSI-MPAR	1.98	0.17	0.70
W.b. Scrubwren	2	TLA+LSI-MNN	0.00	0.53	0.79
	2	TLA+LSI-MNN-MPAR	0.36	0.45	0.79
Grey Currawong	2	TLA+LSI-MNN-MPAR	0.00	0.54	0.76
	2	TLA+LSI-MPAR	1.15	0.31	0.77

*Only models with Akaike weights greater than 0.1 and ROCs higher than 0.6 are shown. The bold type indicates the model with the highest Akaike weight. The sign refers to how the species responds to that landscape characteristic.

The focus for the Mount Lofty Ranges region should be first to mitigate the effects of habitat loss, but as in Villard et al. (1999), the landscape configuration is quite important for many species. Out of 25 species with sufficient models, 12 species had candidate models suggesting that they may adversely be affected by landscapes with high patch isolation and highly linear patches. This is not surprising with native vegetation comprising less than 20% of the region and with a significant proportion of the clearance coming in the last 50 years (Bryan 2000). However, the responses to landscape configuration were quite complex, and it is very difficult to distill any patterns based on taxonomy or natural history.

Some of the results may be spurious; underlying habitat variables not measured in this study but which are correlated with the observed landscape metrics may be truly driving the distribution patterns. It is important to be mindful of the fact that habitat clearance in the region has not been a random process. For example, the White-browed Scrubwren prefers dense riparian habitat, and its occurrence in more fragmented areas may reflect the underlying distribution of riparian areas. Moreover, the White-Naped honeyeater, Striated Thornbill, and Spotted Pardalote are often associated with manna gums (*E. viminalis*). It is not surprising that no model explained occupancy patterns for the Sulfur-crested Cockatoo, Crested Shrike Tit, Rainbow Lorikeet and Laughing Kookaburra. These are wide ranging species and probably respond to the landscape at a much greater scale. The presence of riparian areas (with e.g., *Eucalyptus camaldensis*) would be the main determinant of the distribution of the Crested Shrike Tit. The tree density of riparian woodlands seems to be important for Crested-Shrike Tits (Jansen and Robertson 2001). The Superb Fairy wren is rather ubiquitous in eucalypt woodlands and is probably inured to changes in landscape configuration. It probably is most sensitive to microhabitat vegetation variables, such as the presence of shrub cover (Nias 1984, 1986; Neave et al. 1996). The results illustrate the importance of considering a different landscape scale depending on the species in question. Though a plurality of species responded better to landscape metrics at the 2 km scale (based on

which models had the highest AIC and ROC values), many had candidate models at the 5 km and 10 km scale, and this may be indicative of the dispersal range of the species. That the 10 km scale had greater explanatory power for the Yellow-tailed Black Cockatoo and the rosellas, is not unexpected since they are large-bodied, vagile species. Cockatoos wander over tens of kilometers during the non-breeding season (Saunders 1977). The New Holland Honeyeater and the White-Naped Honeyeater had candidate models at the 10 km scale as well. Being nectarivorous species, they may track the phenology of their nectar sources (Franklin and Noske 1999). The Crescent and Yellow-faced Honeyeaters may forage over smaller scales, as they responded best at the 2 km scale.

These results do not indicate the relative importance of landscape variables compared to patch-level variables. Patch-level variables of vegetation type and structure as well as biophysical variables may be quite important explanatory variables. In a review of 61 studies over a wide array of taxa comparing patch-level variables to landscape variables, Mazerolle and Villard (1999) noted that in over 90% studies, patch-level variables were significant predictors of species abundance or presence or abundance, but that in about 60% of the studies landscape variables were significant predictors. Studies with birds have been rather equivocal. Several have found patch-level variables more important determining factors of species occupancy or abundance (e.g., Berry and Bock 1998, Estades 1999, Mortberg and Wallentinus 2000, Bajema and Lima 2001) while other studies have found landscape variables to be the primary explanatory factors (e.g., Jansson and Agelstam 1999, Saab 1999, Howell et al. 2000, Loyn et al. 2001). In addition, there are interspecific factors. The presence of aggressive honeyeaters, particularly the Noisy Miner (*Manorina melanocephala*) has been shown to be a significant determinant of the bird community in southeastern Australia (Grey et al. 1997, 1998; Ford et al. 2001). Changing landscape structure can alter species interactions (Schmiegelow and Monkkonen 2002), which could affect species distributions. Fragmentation and the changing heterogeneity of the landscape may have synergistic effects on physical, chemical and biotic fluxes that can impinge on species distributions in complex ways (Hobbs 2001). The high model selection uncertainty for many species is probably indicative of the absence of important explanatory variables.

Table 3. Summary of the effects of area, fragmentation, patch shape, and patch isolation on the bird species for 25 species having models with sufficient Akaike weights (> 0.1) and discrimination (ROC > 0.6)*.

Species	AREA	FRAG	PISOLATE	PSHAPE
Striated Thornbill, <i>Acanthiza lineata</i>	++	++	+	--
Brown Thornbill, <i>Acanthiza pusilla</i>	++	++	—	--
Buff-rumped Thornbill, <i>Acanthiza reguloides</i>	++	-	-	-
Eastern Spinebill, <i>Acanthorhynchus tenuirostris</i>	++	++	—	--
Fan-tailed Cuckoo, <i>Cacomantis flabelliformis</i>	++	+	++	-
Yellow-tailed Black-Cockatoo, <i>Calyptorhynchus funereus</i>	++	++	+	-
Shining Bronze-cuckoo, <i>Chrysococcyx lucidus</i>	++	++	-	+
Brown Treecreeper, <i>Climacteris picumnus</i>	++	—	+	-
White-winged Chough, <i>Corcorax melanorhamphos</i>	++	-	—	--
White-throated Treecreeper, <i>Cornobates leucophaeus</i>	++	++	-	--
Musk Lorikeet, <i>Glossopsitta concinna</i>	-	—	+	++
Yellow-faced Honeyeater, <i>Lichenostomus chrysops</i>	++	+	—	--
Whitenaped Honeyeater, <i>Melithreptus lunatus</i>	++	++	-	
Red-browed Finch, <i>Neochmia temporalis</i>	++	-	++	+
Golden Whistler, <i>Pachycephala pectoralis</i>	++	++	-	--
Spotted Pardalote, <i>Pardalotus punctatus</i>	++	—	-	+
Scarlet Robin, <i>Petroica multicolor</i>	++	++	-	--
Brush Bronzewing, <i>Phaps elegans</i>	++	—	—	--
New Holland Honeyeater, <i>Phylidonyris novaehollandiae</i>	--	++	+	
Crescent Honeyeater, <i>Phylidonyris pyrrhoptera</i>	++	++	-	--
Adelaide Rosella, <i>Platycercus elegans</i>	--	++	+	-
Eastern Rosella, <i>Platycercus eximius</i>	++	-	—	++
Grey Fantail, <i>Rhipidura fuliginosa</i>	++	++	+	-
White-browed Scrubwren, <i>Sericornis frontalis</i>	++	++	—	-
Grey Currawong, <i>Strepera versicolor</i>	++	++	—	--

*The sign refers to how the probability of occupancy for that species varies with each landscape characteristic. Double marks refer to responses from the best model, while single marks include all candidate models.

It must be emphasized that response of a species to a landscape with certain mean patch characteristics does not necessarily imply anything about their responses to patch-level variables. Indeed, the classification of species as forest or forest edge species by Howe (1984) is not very informative when making predictions about landscape-level responses. For instance, Howe (1984) classifies the Striated Thornbill, Eastern Spinebill, Brown Treecreeper, White-winged Chough, Red-browed Finch, Scarlet Robin, Adelaide Rosella and Grey Fantail as forest edge species; yet, they do not respond concordantly to the landscape-level metrics. This paper is a cautionary note on extrapolating landscape-level responses from assumed patch-specific responses.

Nevertheless, the results do show that landscape variables alone perform reasonably well in explaining the occupancy patterns of many birds in this region, which was the main thesis of this research. In some cases, patch-level variables can be ignored when building models of species distributions. Many species (15 of 25) have models with ROC values greater than 0.7, which indicates good discrimination. Though it would be ideal to test these models with independent data, they simply do not exist for the region. If one were applying these logistic regression models for predictions in landscape planning, then perhaps it would be necessary to only apply with confidence those models with quite high discrimination. Finally, like all logistic regression analyses, there is the implicit assumption that wherever a species occurs it is suitable breeding and not sink habitat (Pulliam 1988, 1996). If there is a long relaxation time after habitat loss, for instance, the population dynamics may be nonequilibrium and the distribution may not be static. Spatial autocorrelation exists in the data, which may have confounding effects. The observability among different species varies, and we have not taken into account false negative survey errors (Tyre et al. *in review*).

We have shown how the Akaike Information Criterion can be quite useful in statistical inference. Unlike typical inferential techniques, the AIC approach allows one to select a suite of candidate models for which there is good support from the data. By simply selecting the model with lowest AIC (or using likelihood ratio tests in the Fisherian/inferential paradigm), model selection uncertainty is ignored. Indeed for the Mount Lofty Ranges birds one would come up with different conclusions for some species if one only selected the best model. In practice, one could be more or less conservative in selecting a set of candidate models, but here we have chosen to err on the side of caution (model probability $> / = 10\%$) in exploring the effects of landscape configuration on species distribution. Both AIC and ROC can be important techniques in the toolkits of landscape ecologists.

In 1991, the Native Vegetation Act of South Australia was passed, which effectively outlawed the further clearance of native vegetation. There is now a great interest in restoring habitat across the region. Since the species' needs in terms of the spatial configuration of habitat are often quite variable, habitat reconstruction in a strictly qualitative or ad hoc manner is generally not biologically effective nor cost efficient. We are in the process of applying these logistic regression functions of the effect of spatial context on species distributions in simulated annealing algorithms (Metropolis et al. 1953; Kirkpatrick et al. 1983; Possingham et al. 2000; McDonnell et al. 2002) to derive optimal landscape reconstruction scenarios for the avifauna in the Mount Lofty Ranges.

Acknowledgements

This work is partially supported by a US Environmental Protection Agency STAR Fellowship to MIW. Brett Bryan graciously provided the GIS vegetation coverage for the region. Max Possingham extracted the data from an old format and put it into a useable Access database. The Biostatistics group at the Mayo Clinic (Rochester, Minnesota) and Joel Reynolds (Alaska Department of Fish and Game) developed S-Plus scripts for calculating ROC values and performing Mantel tests, respectively, which were very helpful. We would like to thank the Spatial Ecology Lab at the University of Queensland for helpful discussion, and Jessica Redfern and Wayne Getz for useful comments on an earlier version of the manuscript. We are indebted to all the birdwatchers who assiduously conducted surveys for the Adelaide Region Bird Atlas.

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