



Continuum or discrete patch landscape models for savanna birds? Towards a pluralistic approach

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Conceptualising landscapes as a mosaic of discrete habitat patches is fundamental to landscape ecology, metapopulation theory and conservation biology. An emerging question in ecology is: when is the discrete patch model more appropriate than alternative and conceptually appealing models such as the continuum model? There is limited empirical testing of the utility of alternative landscape models compared to the discrete patch model for a range of species. In this paper, we constructed three alternative sets of models for testing the effect of landscape structure on diversity and abundance of a suite of woodland birds in a savanna landscape of northern Australia: the null model (only site-scale habitat variables, landscape context not important), the continuum model, and the discrete patch model. We utilised high-spatial resolution satellite images to quantify spatial gradients in tree cover density (the continuum model), and to then aggregate the fine-scale heterogeneity in tree cover into discrete patches of trees, with grass cover forming the “matrix” (the discrete patch-model). We then evaluated the relative importance of the alternative models using generalised linear models and an information theoretic approach. We found that the importance of the models varied among species, with no single model dominant. Species that move between open grassy areas and woody shelter responded well to the continuum model, reflecting the importance of gradients in density of forage (grasses) and cover (trees), while the discrete model performed best for species that forage in all vegetation strata, and nest predominantly in dense woody vegetation. This finding supports a pluralistic approach, highlighting the need for adopting and testing more than one landscape model in savanna landscapes, and in other landscapes that do not have a well defined patch structure.

The discrete patch paradigm (patch-corridor-matrix model) has been fundamental to conservation biology, metapopulation theory and landscape ecology (Forman 1995). An emerging issue in ecology is the value of alternative landscape models to the discrete patch model including the hierarchical patch dynamics model (Wu and Loucks 1995, Dunn and Majer 2007), the landscape variegation model (McIntyre and Barrett 1992), and continuous models such as the continuum or gradient model. In response to Dunn and Majer’s (2007) claims that a mosaic-based hierarchical patch model can also apply to continuous distributions, Lindenmayer et al. (2007) argue instead for pluralism in landscape models where the appropriateness of a model varies with circumstance. Despite these alternative views, the discrete patch model remains the preferred landscape model with the most extensive empirical testing, while models directly measuring continuous variation in habitat variables remain largely conceptual with limited empirical testing (Fischer and Lindenmayer 2006, Dunn

and Majer 2007). A fundamental, but unanswered question in ecology is: when is the discrete patch model more appropriate than alternative and conceptually appealing models such as the continuum model?

The manner in which habitat is defined is the foundation of a landscape model. Under the discrete model, habitat is a generic concept where habitat patches are defined as discrete landscape elements of similar quality and assumed to be applicable to a range of fauna species (Forman and Godron 1986). The discrete model often considers landscapes to be binary with habitat patches providing foraging, shelter and nesting resources with well-defined patch boundaries which act as a filter to species’ movement. However, the discrete model can also include mosaics of patches of varying habitat quality but still exhibiting clear boundaries (Dunn and Majer 2007, Lindenmayer et al. 2007). In contrast, the continuum model as advocated by Fischer and Lindenmayer (2006) builds on continuum theory (Austin 1985) allowing for

gradual changes in habitat quality through space. The continuum model conceptualises landscapes as having variation across gradients of food, shelter, space and climate (Fischer et al. 2004, Fischer and Lindenmayer 2006). In this model, habitat is defined on a species' specific basis where the forage or shelter gradient may be defined with respect to presence of vegetation elements important for an individual species (e.g. trees and grass cover) (Munks et al. 2007), and a space gradient defined with respect to the spatial arrangement of these elements (Kutt and Woinarski 2007). Fischer et al. (2004) demonstrate the implementation of the habitat contours concept for the greater glider *Petauroides volans*. This approach relies on spatial interpolation to derive contours.

Habitat as a species' specific concept can be defined as "the resources and conditions present in an area that produce occupancy", with the importance of different resources and conditions for individual species varying with scale (Hall et al. 1997). We follow this definition and further define habitat elements as resources and features that are required to provide the necessary food, shelter and space requirements of a species. We build on the habitat suitability and continuum model concept by adopting a similar approach to Fischer et al. (2004) and Fischer and Lindenmayer (2006). We differ however from those approaches in that we use a continuous gridded surface of habitat elements as measured by woody vegetation cover which takes into account small scale heterogeneity and is amenable to spatial analysis (sensu Keitt et al. 2002).

The continuum model is quantitatively challenging as it requires mapping gradients in habitat resources at spatial scales and extents relevant to the ecology of the target species, which may not be known a priori. Current high-spatial resolution remote sensing imagery (down to 0.6 m) is capable of capturing the fine-scale heterogeneity of vegetation cover in continuously varying landscapes (Turner et al. 2003). Advanced spatial analysis techniques are also available to analyse the relationships between landscape heterogeneity and species' distribution patterns (Keitt et al. 2002). Perceptions that the spatial scales of data provided by remote-sensing systems do not match those scales addressed by ecologists has, in the past, restricted collaboration between remote-sensing and ecological researchers (Turner et al. 2003). However, with recent advances in remote sensing, we have the opportunity to develop sophisticated measures of landscape structure at different spatial scales which capture structural gradients in habitat elements.

Tropical savannas are one of the world's most extensive biomes (Huntley and Walker 1982), occurring in regions with a wet-dry tropical climate. The tropical savannas of northern Australia are characterised by gradual environmental variation and widespread ecological connectivity. Unlike many worldwide temperate ecosystems and savannas, Australia's tropical savanna landscapes are in a relatively unmodified condition (Woinarski et al. 2007). Disturbances such as fire, logging/thinning, cycles of drought and rainfall excess, and grazing occur within these landscapes and can be temporally and spatially variable, increasing landscape heterogeneity but rarely resulting in well-defined patch boundaries (Pearson 2002, Woinarski et al. 2005). A patch-dynamic model where rainfall and land management drive savanna heterogeneity is a widely accepted hypothesis

for explaining wildlife distribution and abundance in these savannas (Wiegand et al. 2006). However, the tree-grass structure varies continuously at local to landscape-scales (100s–1000s ha), making Australia's tropical savanna landscapes a suitable candidate for testing the utility of the discrete versus continuum landscape models.

This paper aims to advance recent discussion in the literature on when a discrete patch model or a continuum/continuous gradient landscape model is most appropriate (Lindenmayer et al. 2007). Previous empirical approaches (Fischer et al. 2004) have been species specific and interpolate contours from measures of environmental variables known to be relevant to the species of interest. We contribute to the debate by applying a different empirical approach which measures continuous variation in habitat elements from high-resolution imagery. We investigate the ecological relevance of those measures at differing scales for woodland bird species. We address the question: does a continuum or discrete patch landscape model better explain spatial variation in the diversity and abundance of woodland birds in tropical savanna woodlands of northern Australia? Our focus is "proof of concept" for a suite of woodland birds rather than extensive testing for a range of taxa.

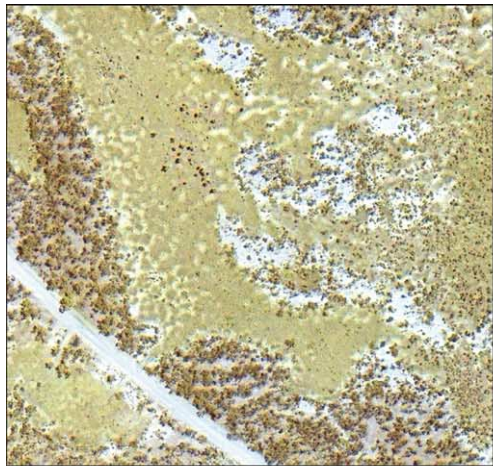
Material and methods

Conceptual model

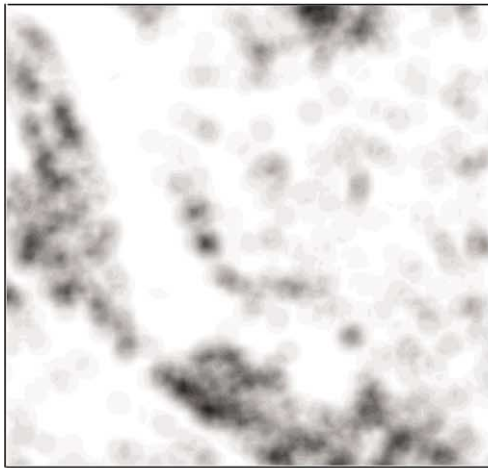
Tropical savanna landscapes are characterised by open woodlands with varying densities of trees and grasses (Fig. 1a). Trees and the underlying grass cover provide the basic food, shelter, nesting and movement resources for woodland birds, the use of these resources varying among species. It is difficult to characterise and map idiosyncratic habitat resources of all woodland bird species occurring in the region (over 100 in total). Rather, we used the spatial variation in tree cover as a surrogate for resource distribution for woodland birds at the landscape scale (sensu Fischer and Lindenmayer 2006).

We conceptualised habitat elements as trees or clumps of trees, which, along with the interspersed clumps of tussock grasses, provide the basic forage and nesting resources for woodland birds. These resources were captured in two alternative models of landscape structure. The first, the continuum model, was derived as a continuous surface of tree cover density with higher values corresponding to dense tree cover (Fig. 1b). The second model, the discrete model, aggregates fine-scale heterogeneity in tree cover into discrete patches of trees as a surrogate for habitat with grass-cover forming the "matrix" (Fig. 1c). These models were then used as a basis for constructing a set of alternative statistical models for testing the effect of landscape structure on woodland birds. In addition to the continuum and discrete models, we also derive a null model which states that the landscape context is not important and contains only site-scale variables.

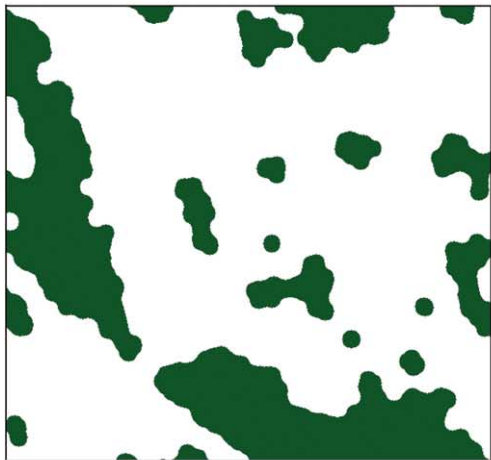
Our versions of both the discrete patch model and the continuum model each represent one simple implementation from many possible implementations. While a discrete-patch model can be implemented in a variety of more



(a)



(b)



(c)

Figure 1. Representation of the conceptual models of a savanna landscape (a) represented as: (b) a continuous surface of tree cover where shading is proportional to tree cover density, and (c) as discrete patches of tree covered area (dark) within a matrix.

sophisticated manners (Dunn and Majer 2007), we chose to use the simple binary implementation of habitat and matrix as it is the most widely used landscape model (Lindenmayer and Fischer 2006).

Model 1 (the “null” model) predicts that site-scale (100s m^2) vegetation factors are best able to explain spatial variation in woodland bird diversity and abundance and that the landscape context ($100\text{--}1000\text{s ha}$) is not important.

Model 2 (the “continuum” model) predicts that gradients in tree cover density (Fig. 1b) are best able to explain spatial variation in woodland bird diversity and abundance.

Model 3 (the “discrete” patch model) predicts that the discrete patches and patch-based metrics can best explain spatial variation in the abundance and diversity of woodland birds (Fig. 1c).

We further postulate that the study species perceive the spatial patterns of resources in savanna landscapes (represented by either the discrete or continuum models) at different spatial scales of influence or ecological neighbourhoods (Addicott et al. 1987). We then infer pattern-process relationships for each species based on the statistical importance of the alternative conceptual models at the different neighbourhood sizes.

Study area

The Desert Uplands bioregion of Queensland, Australia (Fig. 2) has a semi-arid climate with a mean annual rainfall of $350\text{--}600\text{ mm yr}^{-1}$. Vegetation consists predominantly of *Acacia* and *Eucalyptus* woodlands, ephemeral lakes and grasslands (Sattler and Williams 1999). Open *Eucalyptus* woodlands (height $<15\text{ m}$) on sandy soils are dominant ($\sim 85\%$ of the region). However, within these woodlands, there is considerable spatial variation in tree density according to soil type, fire frequency, anthropogenic thinning and drought-related dieback.

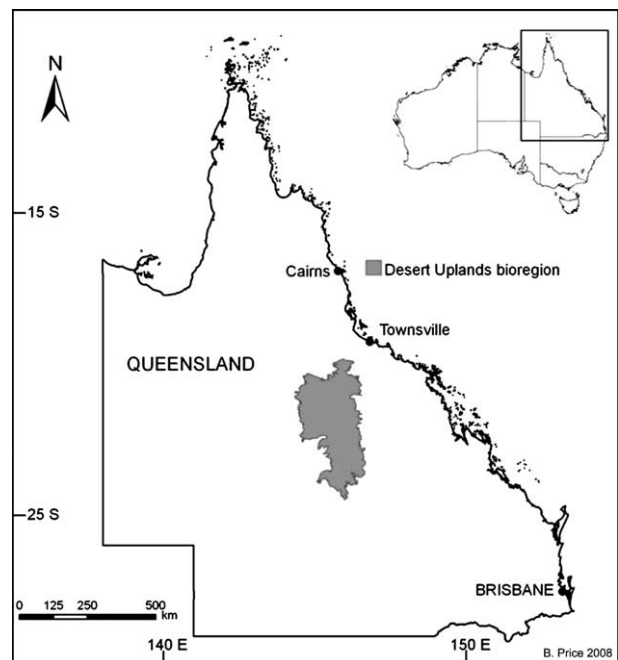


Figure 2. Location of case study area in the Desert Uplands bioregion, Queensland, Australia.

Sites were located in a single regional ecosystem type, (10.3.9, Sattler and Williams 1999), the extensive silver-leaved ironbark *Eucalyptus whitei* woodlands of the northern Prairie-Torrens Creek subregion of the Desert Uplands bioregion of north-eastern Australia. This subregion has a distinct vegetation, geological and geomorphological association characteristic of low-fertility eucalypt savannas. Location of the sites in a same ecosystem type ensured variation in the observed bird pattern was not a function of different vegetation composition.

Bird surveys

Fifty 1-ha sites were sampled between May and June 2004 and resurveyed between March and April 2005. Within each 1-ha site, eight five-minute wandering diurnal bird counts were conducted over a four day period. Each count represented the entire 1-ha area. The observer traversed the central 100 m transect line of the 1-ha plot, recording species seen and heard within a 50 m band on either side of the transect. Two counts of each 1-ha plot were made per day at each site; one count in the morning between dawn and three hours after dawn and the other a minimum of three hours after this period and before dusk. Weather during both survey periods (Australian autumn) was clear and dry, with maximum temperatures between 25 and 30°C and minimum temperatures between 10 and 15°C. This bird survey method has been used extensively in northern Australia's tropical savannas (Woinarski and Ash 2002). In the Australian tropical savanna woodlands, multiple repeated visits including both morning and later counts best account for species richness and abundance as bird activity and pattern is more dispersed spatially and temporally than in wetter woodlands and forests. Two observers with equal bird observation skills visited each site an equal number of times to minimise observer bias (Rosenstock et al. 2002). Both visual and aural observations were recorded. Data used in the analyses were the total summed relative abundance of all the eight counts in each site for both years combined. All sites were located a minimum of 500 m from watering points to standardize the impact of grazing pressure across sites, and as far as practical from fence lines and roads. Sites were separated by a minimum of 1 km. Further information on the sampling methods and site stratification can be found in Tassicker et al. (2006).

In this study we are concerned with differences in the relative abundance, not absolute counts, of bird species within tropical savanna woodland sites. With respect to bird species detectability between treatments, the generally open structure of these savanna woodland sites and the high number of records based on calls rather than sightings minimise the chance of differences in detectability affecting our data and resulting conclusions (Martin and McIntyre 2007).

To take into account both species richness and abundance, we calculated Shannon diversity index (H) (Shannon 1948) for each site as follows:

$$H = - \sum_{i=1}^s p_i \ln p_i$$

where s is the number of species and p_i the relative abundance of each species, calculated as the proportion of individuals of a given species to the total number of individuals in the community n_i/N .

We also selected twelve bird species with varying habitat preferences for testing the alternative models (see Table 1 for scientific names and summary of behavioural patterns).

Vegetation surveys

Habitat variables were measured to act as site-scale variables in each of the conceptual models outlined above following the methods outlined in (Neldner et al. 2005, Eyre et al. 2006). Basal area was measured from two diagonal corners of the 50 × 50 m quadrat for live and dead trees in three diameter categories per species (<5; 5–20; >20 cm), using a Bitterlich gauge, and averaged between corners. From this an estimate of mean basal area for each tree and size class and total live and dead basal area was made. Foliage projective cover was visually estimated for cover for six height classes (0–0.5; 0.5–1; 1–3; 3–5; 5–10; >10 m) with the 0–0.5 height class representing ground vegetation and using seven cover classes (0; <5; 5–10; 10–25; 25–50; 50–75; >75%). Measures of percentage cover of bare earth, rock, litter, grass, sedges, herbs and forbs, and logs (>5 cm) were derived from 20 0.5 m² sub-quadrats in a regular grid within each 50 × 50 m quadrat. Cover is the mean cover score using all 20 quadrats. Total tree, shrub frequency is the number of 0.5 m² quadrats over which a tree or shrub (<1 m) was recorded as present.

We conducted additional vegetation surveys coinciding with capture dates of the IKONOS imagery in January 2007. At 45 sites, 50 × 10 m belt transects were surveyed for foliage projected cover and shrub cover at one metre intervals. Ground cover was recorded in a similar manner categorised as bare soil, litter, woody debris, grass or low-lying shrub.

Image analysis

IKONOS imagery (4 m multispectral spatial resolution, 1 m panchromatic resolution) was acquired in January 2007 (Fig. 1a). We were constrained by the non-availability of archival high resolution imagery data, hence it was not possible to coordinate image capture with the bird surveys. Although tree cover may vary seasonally in savanna environments, our sites were located within low woodland and have low-moderate canopy cover, thus we considered it reasonable to assume tree cover to be relatively stable over the period between image capture in early 2007 and bird surveys in 2004 and 2005.

Following geographic correction to ground-control points, we classified the multi-spectral and panchromatic bands using the software Definiens Professional 5.0 (Definiens AG 2006). We segmented the images into objects such as individual trees, clumps of trees, and grass cover and then using a supervised classification method designated a class to each object in the image as either tree cover, grass cover or bare soil. Classification was derived from the panchromatic band, resulting in a 1 m resolution classification. To obtain a continuous tree cover density

Table 1. Summary of behaviour of individual bird species used as response variables (Higgins et al. 2001, Higgins and Peter 2002, Beruldsen 2003).

Common name	Scientific name	Guild	Foraging	Nesting	Migration
Brown treecreeper	<i>Climacteris picumnus</i> (Temminck)	Foliage insectivore	Forages on tree trunks, branches, fallen timber and ground around base of trees.	Hollows in trunk or branches in large trees.	Resident to sedentary
Budgerigar	<i>Melopsittacus undulates</i> (Shaw)	Granivore	Forages on the ground or directly from seed heads on grass tussocks.	Any small tree hollows or knot holes.	Nomadic, driven by rainfall patterns
Crested bellbird	<i>Oreoica gutturalis</i> (Vigors & Horsfield)	Ground, understorey insectivore	Forages at ground level and in low shrubs and trees.	Broken tree branches (spouts), stump hollows, tree crotch, dense undergrowth (usually <3 m from ground).	Resident to sedentary
Double-barred finch	<i>Taeniopygia bichenovii</i> (Vigors & Horsfield)	Granivore	Forages on the ground or directly from seed heads on grass tussocks.	Shrubs, small trees or grass tussocks <3 m from the ground.	Resident to sedentary
Grey-crowned babbler	<i>Pomatostomus temporalis</i> (Vigors & Horsfield)	Ground and foliage insectivore, omnivore	Forages in all strata, from canopy, trunks, branches, low shrubs and ground.	Tree forks or dense foliage of shrubs and trees from 2 to 15 m above ground.	Resident to sedentary
Rufous whistler	<i>Pachycephala rufiventris</i> (Latham)	Foliage insectivore, nectarivore	Forages in the canopy, sub-canopy trees layer and shrub layer.	Broken tree branches, stump hollows, tree crotch, dense undergrowth (usually <6 m from ground).	Partially resident, and some seasonal breeding migration
Singing honeyeater	<i>Lichenostomus virescens</i> (Vieillot)	Foliage insectivore, nectarivore	Forages predominantly in shrub, mid-strata and canopy trees.	Dense shrubs, saplings, tree branches 2–3 m above the ground level.	Resident to sedentary
Varied sitella	<i>Daphoenositta chrysoptera</i> (Latham)	Foliage/trunk insectivore	Forages on tree trunks, branches and fallen timber.	Tree fork, dead branch of large tree.	Resident to sedentary
Variiegated fairy-wren	<i>Malurus lamberti</i> (Vigors & Horsfield)	Ground, understorey insectivore	Forages among grass tussocks, shrubs, tree bases and low trees.	Thick grass, tussock or shrubs (<1 m from ground).	Resident to sedentary
Weebill	<i>Smicromnis brevirostris</i> (Gould)	Foliage insectivore	Forages in the canopy, sub-canopy trees layer and shrub layer.	Leafy foliage in trees or shrubs, 1–10 m above the ground.	Resident to sedentary
Yellow-throated miner	<i>Manorina flavigula</i> (Gould)	Foliage insectivore, nectarivore	Forages predominantly in canopy and sub-canopy, but also low trees and shrubs.	Dense shrubs, saplings, tree branches 3–5 m above the ground level.	Resident to sedentary
Zebra finch	<i>Taeniopygia guttata</i> (Vieillot)	Granivore	Forages on the ground or directly from seed heads on grass tussocks.	Shrubs, small trees or grass tussocks <3 m from the ground.	Sedentary to nomadic (based on rainfall cycles)

surface (model 2), we passed a filter with a circular window of 15 m radius over the tree cover raster layer in the software ArcGIS version 9.1 (ESRI 2005). We chose a circular window as tree canopies tend to be more circular than rectangular in shape. We selected the 15 m radius filter window after testing a variety of window sizes. This filtering allowed us to create a continuous surface (Fig. 1b) and allowed the model to retain large isolated trees, potentially important resources for birds.

To define the landscape as discrete patches (model 3), we used the GIS algorithm “PatchMorph” (Girvetz and Greco 2007) to delineate patch boundaries from the Definiens raster output of tree cover (Fig. 1c). PatchMorph is a freely available ArcGIS script which defines patches by filtering out areas of low habitat density (in this case low tree cover). Non-suitable areas were included within a patch if they were less than a threshold thickness of 40 m. Patches of tree cover less than a threshold thickness of 40 m and less than a threshold size of 1 ha were excluded (Girvetz and Greco 2007). Thresholds in PatchMorph are set related to the movement behaviour of the species of interest. Since we were modelling species diversity and a range of individual bird species with differing migration and foraging movement patterns, we chose a value large enough to allow contiguous patches to be formed but small enough for small intervening grassy areas and rural roads to split patches.

Explanatory variables

Explanatory variables included site-scale variables and metrics measuring vegetation configuration and composition at the wider landscape context under both the discrete and continuum models (Table 2). Site scale variables were the field vegetation measures obtained for the 50 × 50 m quadrats. We reduced the list of site-scale variables from the available field data a priori to a subset of 12 variables (listed in Table 2) following univariate generalised linear

modelling and ranking according to Akaike’s information criterion (AIC) values (Akaike 1973).

Discrete landscape metrics were derived from the patch-matrix map output (Fig. 1c) of PatchMorph using FRAGSTATS ver. 3.3 (McGarigal and Ene 2003). Continuous metrics were derived from the tree cover density surface (Fig. 1b) using ArcGIS. Both the discrete and continuous metrics were calculated for a series of nested buffer distances (500 m, 1 km, 2 km and 3 km) around each site, thereby allowing us to quantify the landscape context at a variety of spatial neighbourhoods.

We selected continuous and discrete landscape metrics to include simple but comparable measures of the amount of a habitat element (landscape composition) and the spatial arrangement of that element (landscape configuration) where the habitat element in this case was tree cover (Table 2). We chose a priori the following first-order statistics calculated for each buffer distance: 1) continuum model: mean tree cover density (TD), and coefficient of variation in tree cover density (COV); and 2) discrete model: percentage of landscape in tree cover patches (PLAND), patch density (PD), and mean nearest neighbour distance between patches (NN).

Statistical analysis

We used a multivariate generalised linear modelling approach to compare the ability of each of three alternative conceptual models (null model, discrete model and continuous model) to explain the diversity and relative abundance of woodland birds. The response variables were Shannon diversity of birds and the count of 12 individual bird species (Table 1).

High collinearity among variables can lead to high standard errors and difficulties in interpreting parameter estimates in generalised linear models (Graham 2003). Therefore, as a rule, we did not include pairs of variables

Table 2. Summary of site and landscape-scale explanatory variables. Landscape composition refers to variables that measure the amount of a habitat element within a given neighbourhood (in this case 0.5, 1, 2 and 3 km buffers around the site). Landscape configuration refers to variables that measure the spatial arrangement of that element within the same neighbourhood. Discrete variables were derived from the patch matrix representation of the study area and continuous variables from the tree density surface.

	Site scale (50 × 50 m quadrats)	Discrete (at 0.5, 1, 2 and 3 km neighbourhoods)	Continuous (at 0.5, 1, 2 and 3 km neighbourhoods)
Landscape composition	Total basal area (TOTALBA) % Bare earth cover (BARE) % Grassy vegetation cover (GRVEG) % Litter (LITT) % Forbs (FORB) % Log cover Foliage projected cover 5–10 m (FPC5-10) Foliage projected cover over 10 m (FPC >10) Grass frequency (GRFREQ) Shrub frequency (SHRBFREQ) Tree frequency (TREEFREQ) FPC ground vegetation (GRVEGFPC)	Percentage of neighbourhood area in a patch (PLAND)	Mean tree cover density (TD)
Landscape configuration	n/a	Patch density (PD) mean nearest neighbour distance (NN)	Coefficient of variation of tree cover density (COV)

with Spearman pairwise correlation coefficients >0.5 in the same model.

As expected, landscape metrics that measure similar characteristics but at different spatial extents (e.g. tree cover density at 500 m and tree cover density at 1 km) were often highly correlated. Other studies (Schadt et al. 2002, Aguayo et al. 2007) have overcome this problem by creating multiple alternative models and including variables from only one scale in each. However, we were particularly interested in the relative contribution of each scale and the interaction between scales rather than quantifying if one scale was more influential than another. Therefore, to deal with the collinearity, we constructed linear combinations of the variables to be used in place of the variables themselves (Chatterjee and Price 1991). We retained the nested structure of these variables following the approach of Rhodes et al. (2009): if $X_{0.5}$, X_1 , X_2 and X_3 are landscape variables measured at 500 m, 1 km, 2 km and 3 km buffers respectively, then the new variables $Z_{0.5}$, Z_1 , Z_2 and Z_3 were created such that:

$$\begin{aligned}Z_{0.5} &= X_{0.5} - X_1 \\Z_1 &= X_1 - X_2 \\Z_2 &= X_2 - X_3 \\Z_3 &= X_3\end{aligned}$$

This approach reduces metric collinearity and captures landscape effects at the different spatial extents. It provides a novel alternative to the commonly used circular buffers and concentric rings by incorporating the dependence between fine scale and broad scale landscape heterogeneity and its effect on species distributions (see Wiegand and Moloney 2004 for a comparative review of circular buffers and concentric rings).

All models were fitted using R ver. 2.4.1 <www.r-project.org>. The Gaussian distribution was used to model Shannon's diversity index. However, examination of the individual bird count (relative abundance) data revealed the data was zero-inflated, resulting in model overdispersion (Zeileis et al. 2007). We subsequently applied a negative binomial model using the "glm.nb" function in the MASS package of R (Venables and Ripley 2002).

Initially we ranked the effect size of each explanatory variable in a multivariate generalised linear model of each response variable using hierarchical partitioning analysis (Chevan and Sutherland 1991, MacNally 1996) within the R-package "hier.part". Hierarchical partitioning analysis separates the percentage independent and joint contribution of each variable to the total explanatory power of the model (Chevan and Sutherland 1991). There has been some criticism of the use of hierarchical partitioning on correlated variables to determine causal influence (Kruskal 1987, Bring 1995). However, hierarchical partitioning is an accepted practice used widely within ecological literature (Radford and Bennett 2007, Barlow et al. 2008, Johnston et al. 2008, McGill 2008, Tautenhahn et al. 2008). We applied hierarchical partitioning on variables that are not highly correlated to determine independent explanatory power rather than infer causal influence, which is considered a valid approach (Bring 1995, MacNally 1997).

Following this ranking process, we determined an initial subset of 12 site and landscape explanatory variables for each response variable for inclusion in the testing of the

alternative models, with the combination of variables varying among responses.

Next, we developed a set of multivariate generalised linear models for the three alternative conceptual models: set 1 included only site-scale variables (no measures of landscape context); set 2 included site variables plus continuous landscape metrics at a range of spatial extents (0.5, 1, 2, and 3 km buffers); and set 3 included site variables plus discrete landscape metrics at a range of spatial extents. We included site variables in models 2 and 3 as a hierarchy of local and landscape factors were predicted to explain species diversity and abundance. The sets of alternative models included all linear combinations of the subset of 12 explanatory variables for each response variable.

We compared the alternative models by ranking all generalised linear models for all sets (conceptual models 1–3) according to their AIC and Akaike weight (ω_i) (Akaike 1973). The Akaike weights represent the relative likelihood of a model (normalised to sum to 1), given the data and the full set of candidate models (Burnham and Anderson 2002). We conducted a comparison of the support for the best approximating conceptual model by determining the weight of evidence (as measured by the Akaike weight) in favour of model i being the best K-L model compared to the alternative conceptual models. For each response variable, we summed Akaike weights for all model combinations within the 95% confidence set under the null (site variables only) model ($\Sigma\omega_{1i}$), the continuum model ($\Sigma\omega_{2i}$) and the discrete model ($\Sigma\omega_{3i}$), and used these summed weights to compare support for each alternate conceptual model (1–3). Using evidence ratios method (Burnham and Anderson 2002), we determined which conceptual model, if any, was dominant for each response variable.

To test for goodness of fit of the best approximating models for each species, we used a graphical method whereby the standardised residuals were plotted against the half-normal scores and overlaid with a simulated envelope. The model was considered a reasonable fit if the observed residuals followed an approximate straight line and fell within the envelope (Martin et al. 2005). Using R we simulated 19 samples of n observations using the fitted model as if it were a true model. The minimum and maximum values of the n sets of order statistics provided the simulated envelope (Yang and Sun 2006). The resultant half-normal plots revealed that all of the best approximating generalised linear models provided a reasonable fit. For eight of the twelve models, the coefficient of determination (adjusted R^2) of the best fitting models were between 0.3 and 0.55 indicating a good model fit, while the R^2 of the remaining models was between 0.2 and 0.3.

To assess the independent effect of the explanatory variables and their interactions in the final model, we calculated the independent effect size of explanatory variables using hierarchical partitioning analysis (MacNally 1996). Finally, we tested for spatial autocorrelation in the Pearson residuals of the best approximating model. We used Moran's index calculated at twenty 500 m intervals using the Excel add-in ROOKCASE (Sawada 1999). The significance of the Moran's I at each lag distance was calculated using the progressive Bonferroni-corrected level of $\alpha^i = \alpha/k$, where k is the i_{th} lag distance and $\alpha = 0.05$

(Legendre and Legendre 1998). The results showed no significant spatial autocorrelation for any of the final models.

Results

Patterns of landscape influence

The results of generalised linear modelling and comparison of Akaike weights for the three competing conceptual models showed that acceptance or rejection of each “hypothesis” must be on a species by species basis (Table 3). For the varied sittella, model ranking according to the Akaike weights showed that a glm under model 1, the null-model, was the best approximating model. However, for this species, the sum of Akaike weights of all glms in the 95% confidence set under each conceptual model showed slightly greater support for the discrete model but low evidence ratios show high uncertainty in model selection (Burnham and Anderson 2002). Similarly, the evidence ratios suggest there was little difference in support between the continuum and discrete or null models for the double barred finch, variegated fairy wren and Shannon’s diversity index, though the continuum model had the highest Akaike weight. There was stronger support for the landscape context variables for the remaining nine species (Table 3). The continuum model had strong support for the budgerigar, the grey-crowned babbler, the weebill, the yellow throated miner, and the zebra finch while the discrete model had strong support for the brown tree creeper, the crested bellbird, the singing honeyeater, and the rufous whistler.

Effect of site and landscape variables

There was no consistent pattern in the effect of the landscape variables for both the continuum and the discrete model (Table 4). This lack of consistency was apparent both in the most important variables and the most important landscape extents at which they were measured. The landscape variables that were linear combinations of original variables ($Z_{0.5}$, Z_1 , Z_2 , Z_3) measured species response to variability between the smaller and larger buffer extents.

Negative coefficients indicate the species are responding to a higher value of the landscape variable at the larger buffer extent with respect to a comparatively smaller value at the smaller buffer size. Positive coefficient values indicate the opposite effect. For example, a negative response of the yellow throated miner to TD1000-2000, shows that this species is responding to a higher average tree cover density at the 2 km buffer as compared to the 1 km buffer and as such the landscape context at this larger extent is more important than that at the smaller extent for this species.

The independent effect values derived from hierarchical partitioning analysis reveal that overall site variables had a greater influence than variables measuring landscape composition or landscape configuration (Fig. 3). This demonstrates that vegetation structural and compositional attributes in the immediate area of observation rather than landscape context was the most important factor explaining bird abundance and diversity.

Discussion

Recent debate within the ecological literature has addressed the value of a range of landscape models as alternatives to the traditional discrete patch model. In particular, Lindenmayer et al. (2007) have called for a pluralistic approach to landscape models, highlighting that the choice of appropriate model will depend on the landscape, fauna species, scale and goals of the study. Our work has advanced this debate by applying a new quantitative approach to comparing a continuum model and a binary discrete patch model for a variety of woodland bird species in a tropical savanna landscape of northern Australia.

We have focused on woodland birds in a tropical savanna landscape where tree cover and grass cover are the key forage and shelter resources, with the importance of trees versus grass varying among species. We are aware that distribution of tree cover as a resource is only one of many factors (including competition, predation, availability of water etc) that may influence the available space, food and shelter resources of a species. However, by deriving continuous quantitative measures of a key resource (tree cover) we have provided a simple and measurable proxy that

Table 3. Summary of the evaluation of the best approximating conceptual model for each species. Generalised linear models are ranked according to Akaike weight to determine the best model. The proportion of generalized linear models ranked in the 95% confidence set of models for each conceptual model (null, continuum, and discrete), and the sum of the Akaike weight of each glm under each conceptual model (null, continuum, and discrete) within the 95% confidence set of models.

Common name	Best model	%Continuum	%Discrete	%Null	$\Sigma\omega_{Ci}$	$\Sigma\omega_{Di}$	$\Sigma\omega_{Si}$
Varied sittella	Null	0	0.39	0.61	0	0.57	0.38
Brown treecreeper	Discrete	0.67	0.29	0.04	0.04	0.91	0.01
Crested bellbird	Discrete	0	1.0	0	0	0.95	0
Double-barred finch	Discrete	0.26	0.74	0	0.54	0.41	0
Rufous whistler	Discrete	0	1.0	0	0	0.95	0
Singing honeyeater	Discrete	0	1.0	0	0	0.95	0
Budgerigar	Continuum	0.52	0.25	0.23	0.73	0.14	0.08
Grey-crowned babbler	Continuum	0.56	0.35	0.09	0.76	0.16	0.03
Variegated fairy-wren	Continuum	0.51	0.41	0.08	0.71	0.21	0.03
Weebill	Continuum	0.27	0.43	0.30	0.86	0.06	0.03
Yellow-throated miner	Continuum	0.48	0.37	0.15	0.84	0.09	0.02
Zebra finch	Continuum	1.0	0	0	0.95	0	0
Shannon diversity	Continuum	0.33	0.57	0.10	0.61	0.31	0.03

Table 4. Trend and effect size of the most important explanatory variables for each response variable. "Continuous" and "Discrete" indicate best approximating model. + = positive effect size <0.5, ++ positive effect size from 0.5 to 0.99, +++ positive effect size ≥ 1.0 , with a similar pattern for negative (-) effects. Values under landscape composition and landscape configuration indicate buffer sizes in metres.

	Site			Landscape composition						Landscape configuration					
	Ground	Canopy	Bare	500	3000	500-1000	1000-2000	2000-3000	500	3000	500-1000	1000-2000	2000-3000		
Discrete															
Brown treecreeper		++			++										
Crested bellbird	++														
Double-barred finch	+	++													
Rufous whistler	-	++													
Singing honeyeater	++	++													
Varied sitella	+	++													
Continuous															
Budgerigar	++														
Grey-crowned babbler	+		+												
Variegated fairy-wren	-														
Weebill	-														
Yellow-throated miner	+	+													
Zebra finch	+	+													
Shannon diversity	-														

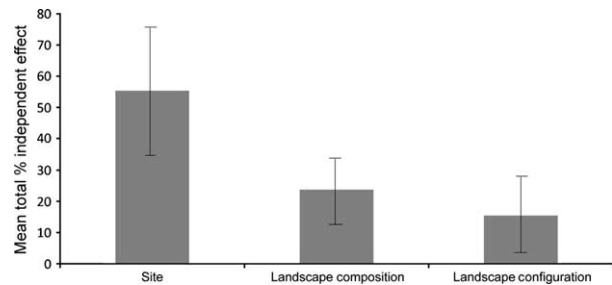


Figure 3. Mean total percentage independent effect for each species and each type of explanatory variable. Error bars indicate standard deviation among the responses of individual species and species diversity.

relates to the space, food and shelter requirements for woodland birds. As such, we have been able to infer some pattern-process-scale relationships influencing woodland birds in a tropical savanna landscape.

Given the relatively intact status of Australia's tropical savannas (Pearson 2002, Woinarski et al. 2007) the continuum model may intuitively be an appropriate model for woodland birds. However, we have shown that this is not always the case and that the most appropriate model depends on both landscape structure and the behaviour of the species under study. Our results therefore support taking a pluralistic approach to landscape modelling.

Taking advantage of high spatial resolution remote sensing technology has enabled us to apply a novel and relevant approach to quantify and empirically test the ecological importance of continuous gradients in habitat elements. Using high resolution remote sensing imagery we were able to take into account fine scale variation in structure of habitat elements at a landscape scale. The model can also account for spatial complexity in the landscape, including valuing "matrix" areas or areas of mixed vegetation composition, which is a key limitation of the discrete model (Kupfer et al. 2006). However, for some species, the binary discrete patch model may better reflect key resources (e.g. stands of dense woodland, areas of more open grassland) and therefore still prove a more appropriate conceptual and quantitative model.

Importantly, although bird species diversity was best predicted by continuous variables, the discrete patch and site models also performed adequately and there was high uncertainty in model selection, suggesting that though different models work well for different species depending on their ecology, general predictions about the entire bird assemblage need to consider landscape gradients, as well as patch and site factors.

Individual species

Adequately capturing ecological complexity in conceptual models is a key to conservation management (Manning et al. 2004). Species' specific differences in habitat use through space, whether represented discretely or continuously, is key to understanding this complexity. In this study, we found that individual species responded differently to the alternative landscape models, according to their behavioural and foraging ecology. For example, the varied

sittella were best predicted by the null-model. This species forages in small to large groups, and is locally nomadic. The varied sittella forms loose foraging groups from 3 to 20 individuals that feed in all levels of the woody vegetation, and they form resident territories (Higgins and Peter 2002). The abundance of this species was best predicted by site factors that represent local feeding resources dependent on tree cover. An alternative explanation is that this species occupies habitats in a “clumped” manner throughout the landscape (i.e. groups of feeding birds) and as such site-based sampling (1-ha counts) will bias the distribution of these species to specific occupied sites.

The discrete patch model performed well for a suite of typical woodland bird species that generally forage in all vegetation strata, and nest predominantly in dense vegetation near the ground. These species occur as pairs with or without non-breeding offspring and utilise all levels of the woody vegetation for foraging and nesting (including ground level). Specifically these species require dense, near-ground shrubs or thickets to nest (Higgins et al. 2001, Higgins and Peter 2002). This suggests that dense tree clumps (mapped as patches) are important and fine scale spatial variation in tree cover is of lesser value. Curiously some of these species have declined (brown treecreeper, crested bellbird) or increased (yellow-throated miners) due to habitat fragmentation in southern Australia (Barrett 2000, Ford et al. 2001). This suggests that species that might respond to patchiness within intact woodlands are more susceptible to tree clearing that superimposes a fragmented mosaic. In this case woodland patches fail to retain sufficient internal resource patchiness for these species.

The remaining suite of species was best predicted by continuous landscape variables. These species were also diverse in behaviour ranging from small canopy species (weebill), gregarious species (grey-crowned babbler), and small species associated with the grass and shrub layer (variegated fairy-wren, zebra finch) (Immelmann 1977, Higgins et al. 2001, Higgins and Peter 2002). All are largely sedentary, except for the zebra finch and budgerigar which respond to rainfall pattern or vegetation disturbance (Immelmann 1977). With the exception of the budgerigar, each species responded well to the coefficient of variation in tree cover density, suggesting that landscape heterogeneity was more important than average tree cover density for these species. The zebra finch and variegated fairy wren forage in open areas, and move quickly between open grassy areas and woody shelter (Higgins et al. 2001, Higgins and Peter 2002). The juxtaposition of these elements at a fine scale is an important determinant of where they are found. Weebills and grey crowned babblers are similarly highly active and vocal, moving in groups quickly between multiple strata and from tree to tree as they forage (Higgins et al. 2001, Higgins and Peter 2002). The yellow-throated miner is a hyper-aggressive bird whose territorial behaviour includes the harassment of other foliage gleaning and nectarivorous birds. This species occupies a mix of open vegetation that allows visual surveillance of territory, dense shrub or understorey for nesting, and diverse vegetation strata for foraging (Higgins et al. 2001).

Significance and future directions

We have demonstrated how high spatial resolution satellite imagery can be successfully used to develop fine-scale quantitative measures of landscape structure relevant to both the continuum and discrete patch landscape models. As such this work highlights how remote sensing can be integrated with biodiversity sciences to gain greater understanding of systems at a wider range of scales (Turner et al. 2003).

The approach to developing quantitative landscape continuum models presented here is relatively simple, considering only two variables related to one habitat element (the tree). We have collapsed the gradients of food, shelter, nesting and movement resources into a single direct measure. Alternative approaches such as point-pattern analysis (Wiegand and Moloney 2004) or spatial statistics (Cressie 1993) may provide further opportunities to model flora and fauna at a more elemental level. The ecological relevance of the approach could be improved if the model incorporated multiple habitat elements measured from high-resolution satellite imagery such as grass cover, shrubs cover and bare soil. In addition, other resources in the landscape such as water availability may be important for many species and could be incorporated into a continuum model validated for a variety of different species. We intend to test our approach further for other fauna groups such as reptiles and mammals.

To fully understand the interrelation between spatial pattern and ecological process in savanna environments, it is necessary to incorporate temporal variability. Future work on testing a quantitative continuum model should therefore include analysis of changes over time. The use of multi-temporal remote sensed imagery has the potential to capture this seasonal variation within the constraints of satellite temporal extent and resolution.

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