

Can multiscale models of species' distribution be generalized from region to region? A case study of the koala

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Summary

1. While various studies have evaluated the habitat requirements for wildlife in fragmented forest landscapes at multiple spatial scales, few have considered whether there is regional variation in the most important factors. This is a conundrum for managers of any species with a broad geographical range: to what extent should studies in one region inform decisions in another?

2. We addressed this question using a case study of the koala, *Phascolarctos cinereus*, in three biogeographically different fragmented forested landscapes in eastern Australia. Mixed-effect logistic models were applied to predict koala occurrence from explanatory variables captured at four spatial scales: the individual tree, the stand (<1 ha), the patch (1–100 ha) and the landscape (100–1000 ha).

3. We used model averaging to account for model and parameter uncertainty, and tested the cross-regional discrimination ability of the models.

4. We discovered that multiscale models of koala distribution cannot be readily generalized from region to region, and that specific conservation actions for each region, rather than the entire geographical range, are more appropriate. We found a strong justification for adopting a hierarchical landscape approach to koala conservation across its range. However, cross-regional differences in habitat relationships occurred within this hierarchy. Exceptions were landscape context, which showed a consistently strong effect and high rank in all regions, and the presence of individual preferred tree species of the genus *Eucalyptus*, which showed modest consistency in its interaction with large-diameter trees across the regions. In contrast, the remaining habitat variables, including patch size (a key management factor), showed moderate to strong cross-regional variation attributed to the interaction of edaphic factors, landscape history and contemporary land-use patterns.

5. *Synthesis and applications.* Adopting a uniform conservation programme over a large geographical area is attractive to policy-makers and conservation planners. However, our study confirms the lack of generality of species distribution models over large areas. Consequently, we argue against adopting a uniform conservation programme for species with a large geographical range.

Key-words: cross-regional prediction, forest fragmentation, habitat loss, geographical range, landscape context, mixed-effect model, wildlife conservation over large area

Introduction

Comparative biogeographical and ecological studies have revealed considerable variation in the size, shape, boundary and internal structure of the contemporary geographical

ranges of species (Brown, Stevens & Kaufman 1996; Gaston 2003). While many species have small ranges, and a few have very large ones, an important component of the world's terrestrial fauna have natural geographical ranges extending over many regions, for example, neotropical birds of North America (DeGraff & Rappole 1995). Regional variation in habitat relationships within such broad geographical ranges is

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an emerging issue in ecology. A recent study by Whittingham *et al.* (2007) found that predictors of lowland farmland birds in one region of England tended to have different effects in other regions. Regional variation in habitat relationships is particularly important for forest fauna, the habitats often being subject to different levels of human modification in different landscapes (Laurance & Bierregaarde 1997; Rochelle, Lehmann & Wisniewski 1999). For fragmented forests, we need to understand habitat relationships within individual landscapes, while at the same time seeking general guidelines that can be applied across broad geographical ranges. This vital issue has yet to receive detailed attention from conservation practitioners, who tend to rely on simple rules, such as protecting large patches, as being obviously correct and uniformly applicable over multiple regions.

In fragmented landscapes, the relationship between pattern, process and scale is integral to understanding fauna–habitat relationships (Pearson *et al.* 1996; Saab 1999). Ecologists now realize that the distribution patterns of species cannot be explained at a single spatial scale, and that landscape-scale heterogeneity influences the occurrence of species at finer spatial scales (Pearson *et al.* 1996; Wiens 1997). Two ecological views of landscape heterogeneity are particularly relevant to the conservation of wildlife populations in fragmented landscapes. The first is the metapopulation model, which considers metapopulation persistence in terms of the dynamics of local extinctions and colonizations in a binary patch–matrix landscape (Hanski 1999). The second is landscape ecology, which emphasizes landscape mosaics with multiple habitat types of varying quality, spatial variations in patch quality, patch context and connectivity among patches (Wiens 1997). The application of these concepts requires a focus on matching the scale of ecological processes with the patterns of species' occurrence in landscape mosaics (Pearson *et al.* 1996). Mosaic landscapes do not fit the patch–matrix model, and are more suitable to the landscape approach (Wiens 1997). We adopted a hierarchical landscape approach in this study.

The koala, *Phascolarctos cinereus* (Goldfuss), is an ideal species for identifying similarities and differences in pattern–process–scale relationships within fragmented forest landscapes across a broad geographical range. It is widely distributed in eastern Australia, extending over 30 biogeographical regions from tropical Queensland (18°S) to temperate Victoria and south-east South Australia (38°S). Previous studies have reported sensitivity to both fine-scale habitat structure, its composition and landscape structure (Moore & Foley 2005; McAlpine *et al.* 2006; Rhodes *et al.* 2006). Moore & Foley (2005) found that tree foliar chemistry restricts the use of trees by koalas, and thus limits food availability and potentially influences their distribution. Rhodes *et al.* (2006) separated the effect of natural habitat quality and anthropogenic impacts on koala distribution in a fragmented semi-urban landscape on the central coast of New South Wales. They concluded that the amount and connectivity of high-quality habitat had the strongest effect, with anthropogenic impacts having an important secondary impact. McAlpine *et al.* (2006) quantified the effect of the area of forest habitat and its spatial configuration

on koala populations in a fragmented semi-urban landscape in south-east Queensland. They concluded that habitat area had a strongly independent effect, with the interaction between habitat area and configuration also being important. A critical question is: how general are these results? Do we need studies of koala habitat relationships in all regions to make well informed management decisions, or are relationships similar across the koala's entire geographic range? This is a problem for managers of all species that have a broad geographical range: to what extent do studies in one region correctly inform decisions in another?

We used the koala as a case study to address the question: can multiscale models of species distribution be generalized from region to region? Using tree-scale data on the presence/absence of koalas, we applied a cross-regional, hierarchical modelling approach to determine the relative importance of habitat variables, ranging from the individual tree (1–10s m²) to the surrounding landscape (100s–1000s ha) in three fragmented forest landscapes of eastern Australia. We also tested the cross-regional predictability of the models using the area under the receiver operating characteristic (ROC) curve. We discovered important regional differences in the effect size and rank of most variables, while the cross-regional predictability of the hierarchical models was low to moderate.

Methods

STUDY REGIONS

The study focused on three local government areas in three different states in coastal eastern Australia: Noosa in south-east Queensland, Port Stephens on the central coast of New South Wales, and Ballarat in central western Victoria (Fig. 1). Port Stephens is ≈700 km south of Noosa, and Ballarat is ≈900 km south-west of Port Stephens. These biogeographically different regions support significant koala populations, have a mixed rural–urban land use, and a history of habitat loss associated with European settlement. Noosa has a subtropical coastal climate, with native vegetation ranging from coastal heath to wet and dry eucalypt forests and subtropical rainforests. Over 50% of eucalypt forests, the main habitat for koalas, has been cleared for farming and urban development (Seabrook *et al.* 2003). Port Stephens was settled early in the 19th century, with clearing of eucalypt forests starting on the fertile alluvial soils in western parts of the local government area (Knott *et al.* 1998). Contemporary landscape change is concentrated in the coastal landscapes, driven by pressure for urban development, with the remaining koala populations concentrated on the less fertile, sandy soils (Lunney *et al.* 1998). Ballarat has a temperate climate and a land-use history of gold mining, agriculture and urban settlement dating back to 1851. Remaining eucalypt forests are predominantly on relatively infertile soils, with only small areas on more fertile, volcanic-derived substrates. The Ballarat koala population was thought to be largely extinct by the early 1900s, mainly due to hunting and clearing, but since the 1940s it has been replenished through translocations from coastal island populations (ANZECC 1998).

CONCEPTUAL MODEL

In building predictive models of species distribution, a first step is to develop a conceptual model of species–environment relationships

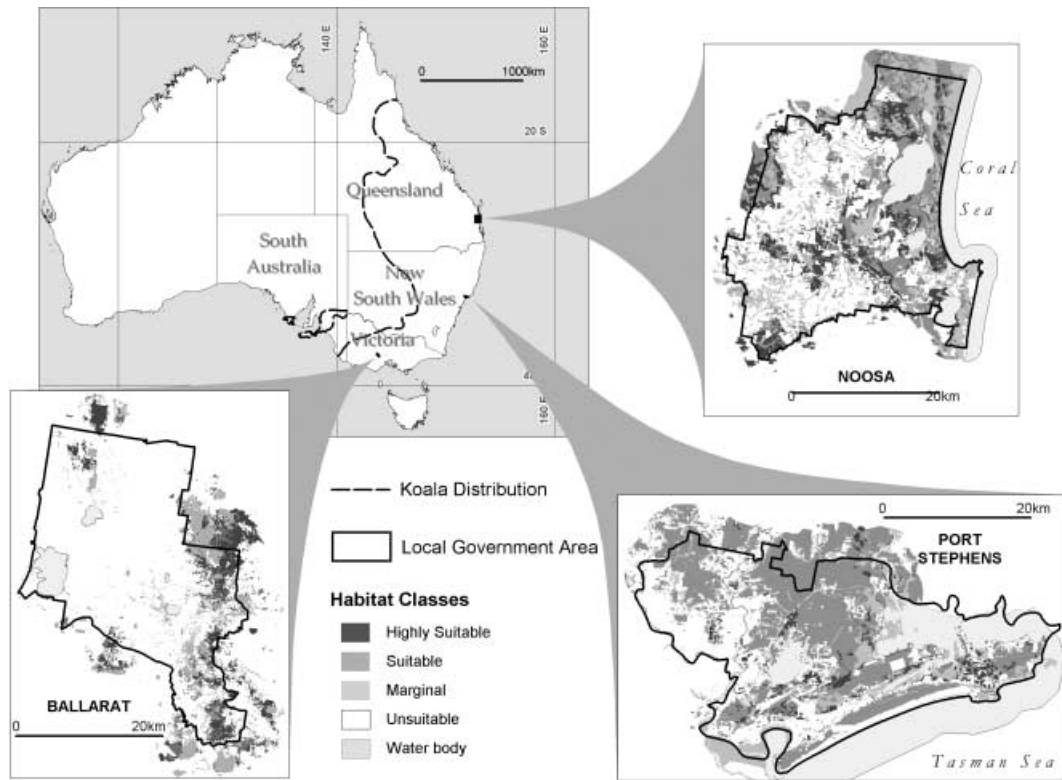


Fig. 1. Location of the study regions and the geographic range of the koala.

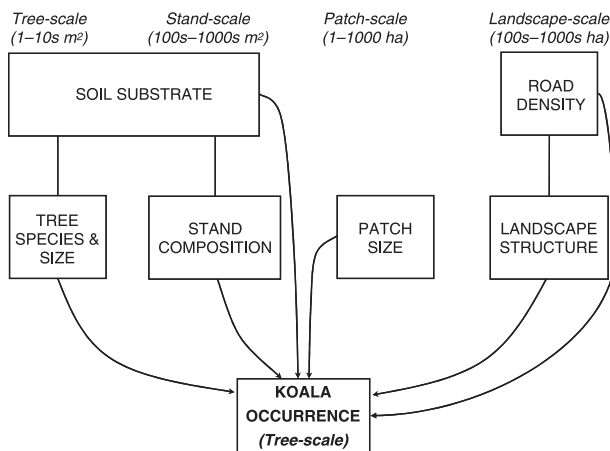


Fig. 2. Multiscale conceptual model of the habitat and abiotic factors influencing occurrence of koalas in fragmented forest landscapes of eastern Australia.

(Guisan *et al.* 2006). We present a multiscale conceptual model of the factors influencing the occurrence of koalas within fragmented forest landscapes (Fig. 2). The scale of the individual tree and site were taken to represent a koala's perception of habitat quality, as defined by its daily foraging movements within its home range (1–100 ha). Within their home range, koalas actively select individual tree species and forest stands with a high proportion of preferred tree species of the genus *Eucalyptus* (Phillips, Callaghan & Thompson 2000; Rhodes *et al.* 2005; Matthews *et al.* 2007), often occurring on the more fertile soils. At the coarser patch (1–1000s ha) and landscape scales, the distribution of individuals across the landscape is directly linked to species' persistence. The smaller the patch, the

Table 1. Classification of habitat-quality classes based on the proportion of overstorey eucalypt tree species and the function of each class (modified from McAlpine *et al.* 2006)

Habitat quality class	Habitat tree rank (% of overstorey)		
	Eucalypt species:		
	Primary	Primary and secondary	Secondary
Highly suitable	≥30	≥50	≥50
Suitable	10 < 30	30 < 50	10 < 50
Marginal	< 10	<30	<10
Unsuitable	Scattered trees	Scattered trees	Scattered trees

greater the habitat loss and more fragmented the landscape, the more limited are the available resources, and the greater the likelihood of external threats to survival and reproduction. The different scales of observation (tree, site, patch or landscape) therefore represent varying pattern–process relationships important for koalas.

HABITAT MAPPING

For each study region we used the *Koala Habitat Atlas* (Lunney *et al.* 1998; Australian Koala Foundation, unpublished data), prepared by the Australian Koala Foundation, to map four koala habitat suitability classes: highly suitable, suitable, marginal and unsuitable (Table 1). The *Atlas* was derived primarily from vegetation communities interpreted from aerial photographs and ground surveys. To account for adjoining habitat patches, and patches extending beyond the study region, we extended the external boundary

of each study region by 5 km. The habitat suitability class for each vegetation community was assigned using the proportional abundance of the preferred (primary and secondary) habitat (food and shelter) tree species identified (Table S1 in Supplementary Material). The tree species were different for each study area. A primary koala habitat tree is a *Eucalyptus* species with a significantly higher proportion of trees having one or more koala faecal pellets around its base (an indicator of use), compared with other tree species. A secondary habitat tree is a *Eucalyptus* species that registers a significantly higher proportion of trees with pellets compared with that observed for remaining species (excluding primary species). A third category, supplementary habitat tree species, records a significantly lower proportion of trees with pellets than for secondary species, but greater than for other tree species, which generally lack evidence of use by koalas (Phillips, Callaghan & Thompson 2000). Non-*Eucalyptus* species also provide supplementary food and shelter resources but, more importantly, they provide additional shelter for koalas, particularly from harsh weather.

PRESENCE/ABSENCE DATA

Surveys were conducted during the winter and spring of 2001/02 for Noosa, autumn 2002 for Port Stephens, and autumn 2003 for Ballarat. The koala remains active all year round, with no suggestion that habitat selection or tree choice varies with the season (Martin & Handasyde 1999). Thus time of year of surveys is not expected to influence the results. A combination of a random stratified and Latin hypercube designs were used to select koala survey sites for each region (McKay, Beckman & Conover 1979). An initial pilot survey of 60 sites was conducted for Noosa, with sites clustered in groups of four at 250-m intervals. For all remaining surveys, a grid of sites at 750-m intervals was generated, with a subset of sites selected according to patch habitat quality, patch size, distance to sealed roads, and the proximity of neighbouring habitat patches of similar quality. Sampling concentrated on the highly suitable and suitable habitat classes, with larger habitat patches sampled multiple times to take into account internal variation in habitat resources. Sites affected by intense wildfires were not surveyed. Some adjustment was made to the final selection of sites due to logistical constraints.

Koalas are difficult to see in the wild. For this reason, we undertook surveys for the presence or absence of koala pellets around the base of individual trees. Their distinctive faecal pellets provide a reliable and repeatable index of koala presence. A 1-m catchment around the base of each tree (with a minimum diameter at breast height of 10 cm) was searched for two person-minutes, or until a koala pellet was found, for a sample of 30 trees (nearest to the site centre). A presence was recorded for each tree where one or more koala pellets were found. A total of 5850 trees were sampled at 195 sites for Noosa, 2400 trees at 80 sites for Port Stephens, and 3000 trees at 100 sites for Ballarat. Reasonably long pellet longevity, estimated to be in the order of several months on average in Port Stephens (J.R.R. and co-workers, unpublished data), allowed us to assume that low detectability, caused by rapid pellet decay, was not an issue in our field programme.

EXPLANATORY VARIABLES

A common feature of species distribution modelling is that there are often many candidate predictor variables (Rushton, Ormerod & Kerby 2004). We selected, *a priori*, nine explanatory variables for each study region based on the conceptual model as well as previous research by Rhodes *et al.* (2006) and McAlpine *et al.* (2006). Tree species and tree basal area at breast height were recorded for each tree

surveyed. Tree species were grouped into primary, secondary, supplementary and other preference classes (Table S1) based on proportional use (Phillips, Callaghan & Thompson 2000). At the stand scale, we calculated the proportion of primary tree species and soil substrate classes derived from classified geology mapping for each region at a cartographic scale of 1 : 100 000. Parent geology is one of the fundamental determinants of soil type. The geological units were assigned to four broad soil substrate classes: sand, sandy loam, clay loam and clay, with ordinal rankings assigned to each class based on relative fertility.

At the patch scale, we chose patch size as the key explanatory variable. At the landscape scale, FRAGSTATS ver. 3 (McGarigal *et al.* 2004) was used to quantify the percentage of the landscape (excluding water bodies) occupied by highly suitable habitat at five radial spatial extents (1, 2, 3, 4 and 5 km) from each survey site (Table S2). The density of sealed roads within each radial extent was calculated using ARCGIS ver. 9 (ESRI 2004).

We also chose, *a priori*, an inverse distance-weighted habitat metric, based on previous work by Rhodes *et al.* (2006). The metric quantifies the combined influence of the amount of habitat and its connectivity. It is essentially a distance-weighted mean of the habitat values around each site with the weighting following a negative-exponential decline with distance from a survey site. This metric was calculated for highly suitable plus suitable habitat, from binary raster grids classified as: 1 = highly suitable or suitable habitat; 0 = other and cleared habitat; water = no data. The negative-exponential weighting function was scaled to have a mean of 5750 m; approximately the 75th percentile koala dispersal distance estimated from an empirical data set (Rhodes *et al.* 2006). In Port Stephens, Rhodes *et al.* (2006) found that this scaling had more explanatory power for koala distributions than scaling to mean dispersal distances or home-range movements.

STATISTICAL MODELLING

Explanatory variables for each study region were standardized to have a mean of 0 and a SD of 1. Spearman's rank correlation was applied to test for collinearity between variables at each scale. Booth, Nicolucci & Schuster (1994) suggest that, if a pair of variables has a correlation coefficient >0.5, then they should be considered proxies of one another and one of the variables should be removed. We followed this rule of thumb.

Mixed-effects logistic models were used to assess the effect of explanatory variables at each scale of influence. Models were fitted independently for each study region. Mixed-effects models are used primarily to quantify relationships between a response variable and covariates in data that are grouped according to one or more classification factors, and are useful for analysing hierarchically structured phenomena (Pinheiro & Bates 2000). For example, Buckley, Briebe & Rees (2003) applied mixed models to analyse how environmental and intrinsic variables affect growth and reproduction of invasive plants. By associating common 'random' effects to observations sharing the same level of the classification factor, mixed-effects models flexibly represent the covariance structure induced by grouping in the data. In our koala study, the mixed-effects models accounted for the correlation between neighbouring trees within a site (the classification factor) by including an intercept random effect between sites. The models had the general form:

$$\ln\left(\frac{p_{ij}}{1-p_{ij}}\right) = \beta'X_{ij} + b_i \quad \text{eqn 1}$$

where p_{ij} is the probability of koala presence at tree j in site i ; β is a vector of coefficients; X_{ij} is a vector of explanatory variables for tree j in site i ; and b_i is a normally distributed random effect for site i , with a mean of zero and variance σ^2 .

We modelled the probability of koala presence using the R ver. 2.2.0 package 'glmmML' (R Project for Statistical Computing, <http://www.r-project.org>). We compared models using Akaike's information criterion (AIC) (Burnham & Anderson 2002), where AIC was calculated as:

$$\text{AIC} = 2L + 2K \quad \text{eqn 2}$$

where L is the marginal negative log-likelihood of the model and K is the number of parameters in the model. This formulation of AIC, using the marginal likelihood, is appropriate for mixed-effects models where the modelling focus is at the population level, as in this study (*sensu* Vaida & Blanchard 2005).

For the proportion of highly suitable habitat and road density, we investigated how the Akaike weight (w_m) of the univariate model varied at each spatial extent to determine if one extent had a high level of support. The Akaike weight of model m is a measure of the probability that it is the Kullback–Leibler best model, given a set of models, with $w_m > 0.9$ indicating a high level of support for a candidate model (Burnham & Anderson 2002).

We constructed a set of alternative models from all linear combinations (number of models = 512) of the nine explanatory variables for each study region, including the interaction between tree species and tree basal area. We then ranked these models by their AIC values and calculated the Akaike weight for each model. We also constructed a 95% confidence set of models by starting with the model with the highest Akaike weight and repeatedly adding the model with the next highest weight until the cumulative sum of weights exceeded 0.95 (Burnham & Anderson 2002).

The direction and magnitude of the effect size of each explanatory variable was determined based on model-averaged parameter estimates, calculated using the average of the coefficient estimates from all models, weighted by w_m (Burnham & Anderson 2002). We quantified parameter uncertainty by calculating the unconditional SE of the parameter estimates (Burnham & Anderson 2002, p. 162). To quantify the relative importance of the explanatory variables, we summed the Akaike weights (Σw_m) from all model combinations where the variable occurred. We then ranked the explanatory variables according to Σw_m ; the larger the weight value, the more important the variable was relative to the others.

MODEL FIT AND DISCRIMINATION ABILITY

We also tested for spatial autocorrelation in the model residuals, averaged to the site scale and incrementally calculated at $20 \times 500\text{-m}$ intervals using the EXCEL add-in ROOKCASE (Sawada 1999). The significance of 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 & Legendre 1998, p. 671).

The fit of the model containing all explanatory variables for each study region was assessed using a Pearson χ^2 goodness-of-fit test, with the P value calculated from a normal approximation of the Pearson χ^2 statistic distribution (Hosmer & Lemeshow 2000). The discrimination ability of each model was assessed using the area under the receiver operating characteristic (ROC) curve (AUC) (Pearce & Ferrier 2000), and applied in a cross-validation procedure to test its ability to discriminate correctly between presence and absence for that region. The cross-validation procedure consisted of

randomly splitting the data into 10 equal-sized groups. For each group, $s = 1, \dots, 10$, the model was fitted to the data in the other nine groups and then predictions were made for group s . This was repeated for each group, then the AUC was calculated using the R ver. 2.2.0 package ROC (BioConductor Project, <http://www.bioconductor.org>). This procedure was replicated 100 times, and the mean and upper and lower 95% CI of the AUC were used as a cross-validation measure of the discrimination ability of the model. If the lower 95% CI does not include the 0.5 value, then there is evidence the model has an ability to discriminate between the two groups (Hanley & McNeil 1982). We also conducted cross-regional validation of model discrimination ability by applying the full model of all explanatory variables to the data sets for the other regions. Because of regional differences in data set size, a randomly selected subset of the Noosa and Ballarat data was assigned to 80 sites, 2400 trees, corresponding to the size of data for Port Stephens. The cross-validation procedure was then applied across all regions.

Results

PATTERNS OF OCCURRENCE

There was considerable regional variation in the overall proportion of all trees that recorded koala presence (Fig. S1, see Supplementary material), with Noosa (12%) and Ballarat (16%) having relatively low rates of tree use compared with Port Stephens, where 43% of trees recorded presence. There was also considerable variation in the proportion of trees with koalas present for each tree preference category, with koalas recorded for 55% of primary habitat trees in Port Stephens compared with 41% for Ballarat and 24% for Noosa. In all regions, the percentage of secondary, supplementary and other tree categories associated with koalas was lower when compared to primary trees. In Port Stephens, the observed use of supplementary and other tree species was higher than in Noosa and Ballarat.

SPATIAL EXTENTS AND COLINEARITY

For Noosa, comparison of the Akaike weights strongly indicated that 1 km was the appropriate spatial extent for both the proportion of highly suitable habitat and the density of roads. For Port Stephens, there was weak support for the proportion of highly suitable habitat at the 2 km extent and road density at the 4 km extent. For Ballarat, the proportion of highly suitable habitat and road density showed a similar level of support at all spatial extents. We subsequently chose the 1 km extent for both variables to allow for data consistency in cross-regional predictions. The final explanatory variables showed an acceptable level of colinearity for all regions ($P < 0.05$).

PATTERNS OF INFLUENCE

The effect size and level of parameter uncertainty of the explanatory variables varied among regions (Fig. 3). For Noosa, the distance-weighted habitat metric had the strongest effect of the nine explanatory variables, while the proportion of highly suitable habitat also had a strongly positive effect (Fig. 3a). Tree basal area, tree species, and their interaction

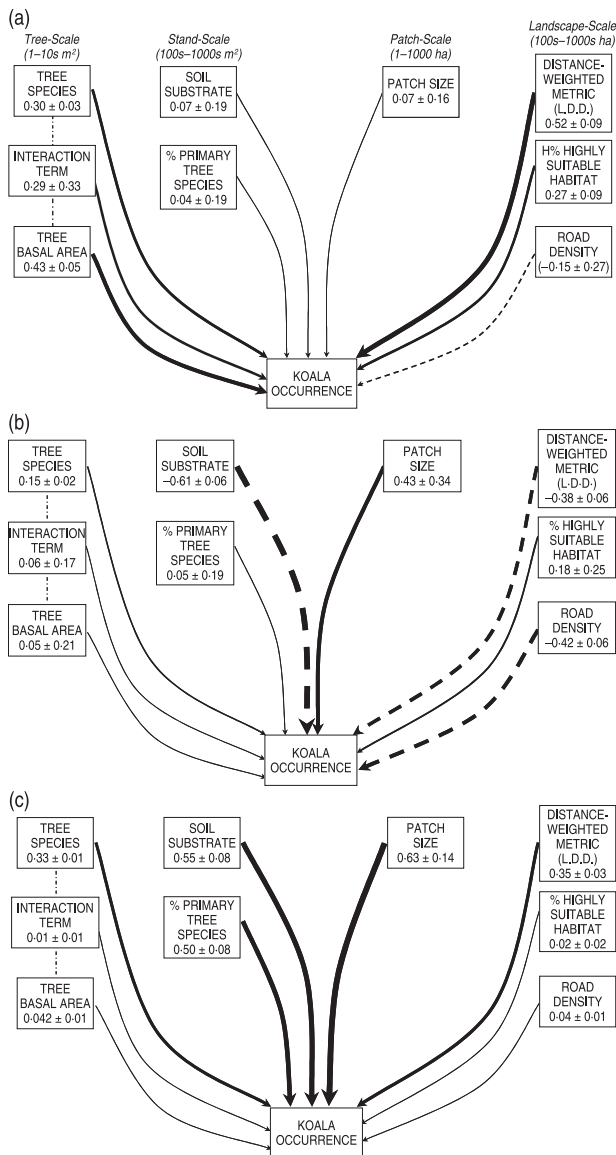


Fig. 3. Path diagrams showing the effect of the most important explanatory variables at each organizational scale on occurrence of koalas observed at the tree scale for: (a) Noosa; (b) Port Stephens; (c) Ballarat. Line width is weighted by the model-averaged standardised parameter values in the mixed-effects logistic models. Dashed lines, negative effect; dashed-dotted lines, interaction effects. Parameter estimates and unconditional SE of the parameter estimate are shown in the text box along with the variable name. L.D.D. = long distance dispersal.

term also had a strong effect on the probability of koala occurrence, with the positive interaction effect indicating that the importance of the effect size of tree species increased with tree basal area. There was low parameter uncertainty for tree species and tree basal area, while the uncertainty for the interaction term was high. Soil substrate, proportion of primary tree species, patch size and road density had weak effects on koala occurrence and high parameter uncertainty. Model uncertainty was moderate, with 17 of the 512 models in the 95% confidence model set. There was no evidence for a significant lack of fit for the model containing all explanatory

variables ($Z = -1.854$, $P = 0.064$). Spatial autocorrelation at the 500, 2000 and 5000 m lag distances was significant (Fig. S2a, see Supplementary material).

For Port Stephens, patch size had a strongly positive effect, while the distance-weighted habitat metric and road density both had moderately strongly negative effects (Fig. 3b). The proportion of highly suitable habitat had a more weakly positive effect. Tree species and the proportion of primary tree species at the stand scale had a moderate positive effect, while tree basal area and the interaction term had weakly positive effects. Soil substrate had a strongly negative effect, indicating that the probability of koala presence was higher on the coastal sandy soils relative to clay loam and clay soils. There was considerable model uncertainty with 55 of the 512 models in the 95% confidence set. There was no evidence for a significant lack of fit for the full model containing all explanatory variables ($Z = -0.314$, $P = 0.753$). The Z -normal of Moran's I was not significant at all lag distances (Fig. S2b, see Supplementary material).

For Ballarat, patch size had a strongly positive effect, the strongest of all variables. Tree species also had a strong positive effect, while tree basal area and the interaction term both had weakly positive effects (Fig. 3c). At the stand scale, soil substrate and the proportion of primary tree species had a strongly positive effect. The distance-weighted habitat metric had a strongly positive effect, while the proportion of highly suitable habitat and road density had a weakly positive effect. There was considerable model uncertainty, with 69 of the 512 models in the 95% confidence set. There was a significant lack of fit of the full model containing all explanatory variables ($Z = 2.99$, $P = 0.003$). The Z -normal of Moran's I was not significant at all lag distances (Fig. S2c, see Supplementary material).

VARIABLE RANKING

For Noosa, ranking of the explanatory variables according to Σw_m across all model combinations showed that tree basal area and tree species had the highest rank (Fig. 4a). The distance-weighted habitat metric and the proportion of highly suitable habitat had the next highest rank, highlighting the importance of landscape context for koalas in Noosa. The interaction of tree species and tree basal area, road density, patch size, soil substrate and the proportion of primary tree species had the lowest rank in that order.

For Port Stephens, soil substrate, road density, the distance-weighted habitat metric and patch size had the highest ranking (Fig. 4b). Tree species, the proportion of highly suitable habitat (4 km extent), tree basal area and the interaction of tree species and tree basal area were ranked next. The proportion of primary tree species at the stand scale had the lowest rank.

For Ballarat, tree species, soil substrate and the proportion of primary tree species at the stand scale had the highest rank (Fig. 4c). The distance-weighted habitat metric and patch size had the next highest rank, followed by tree basal area and the interaction of tree species and tree basal area. Road density and the proportion of highly suitable habitat had the lowest rank.

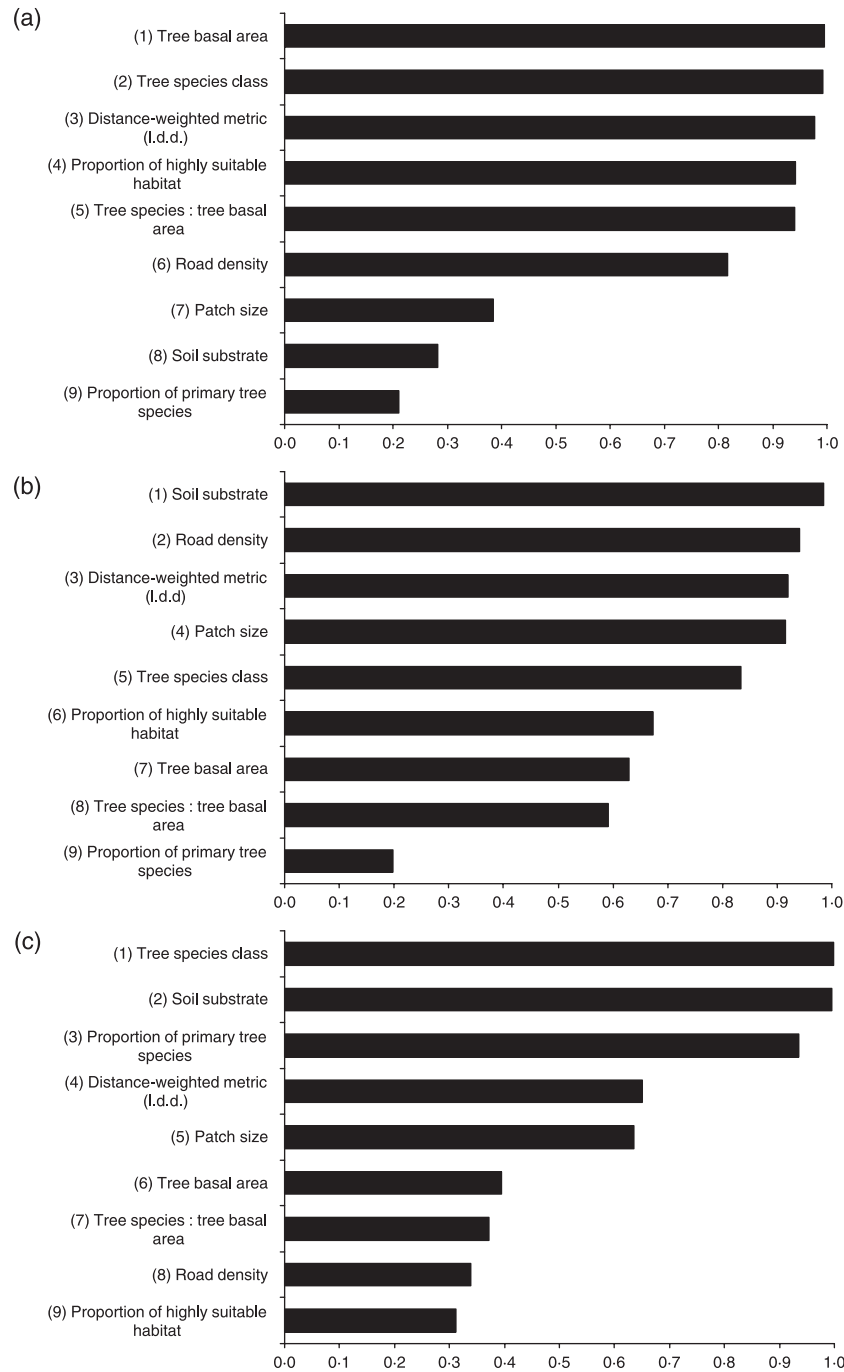


Fig. 4. Ranking of the importance of explanatory variables and their interactions according to the sum of the Akaike weights (Σw_i). (a) Noosa; (b) Port Stephens; (c) Ballarat. L.D.D. = long distance dispersal.

MODEL DISCRIMINATION

The discrimination ability of the full models, as indicated by the AUC of the ROC, varied from low for Noosa (95% confidence 0.63–0.67) and Port Stephens (95% confidence 0.67–0.70) to moderate for Ballarat (95% confidence 0.72–0.73) (Fig. 5). The predictive performance of the models was low to moderate wherever they were applied. The reciprocal application of the Port Stephens and Ballarat models had moderate discrimination ability (Fig. 5). In contrast, the Noosa model showed the weakest cross-regional predictability, especially when applied

to the Ballarat data set, while the Ballarat model showed a corresponding low predictability when applied to Noosa.

Discussion

MODEL TRANSFERABILITY

In recent years, predictive modelling of species distributions has become an increasingly important tool to address questions in ecology, biogeography, conservation biology and the impact of future climate on biodiversity (Guisan & Thuiller

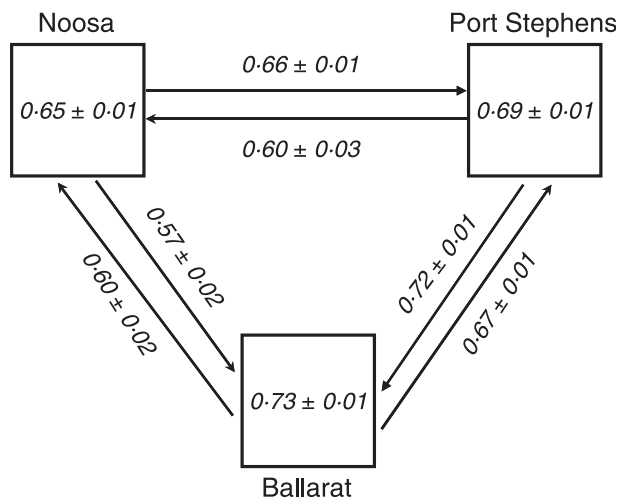


Fig. 5. Graphic summary of AUC for the full models for each region and the cross-regional application of these models to the other study regions. (a) Noosa; (b) Port Stephens; (c) Ballarat. Arrows indicate the direction of the cross-regional application of each model.

2005). Considerable progress has been made in addressing these questions at multiple spatial scales (Saab 1999; Fuhlendorf *et al.* 2002), but the more focused question of cross-regional transferability of predictive species distribution models has received little attention. However, a few studies provide a comparison to our koala study. Vanreusel, Maes & Van Dyck (2007) found that resource-based predictive models of butterflies in the Campine region of Belgium showed high levels of transferability among adjacent areas. The Belgian study was located in one ecoregion, thus the different areas shared a similar climate, general topography, soil type and vegetation types. In contrast, Fielding & Haworth (1995) found a lack of cross-regional generality for distribution models of three bird species for five adjacent study areas in western Scotland and adjacent islands. Whittingham *et al.* (2007), in a study of lowland farmland birds in England, also concluded that models were not generally transferable across regions, with

total model fit being poor. In our study, the low-to-moderate cross-regional predictability of the distribution models was not unexpected, given the biogeographical and land-use differences among the regions. This was indicated by the low cross-regional AUC values (0.57–0.72), which were typically lower than the internal tests. Our study further confirms the lack of generality of species distribution models over large areas, and identifies the need for ecologists and conservation managers to be careful about applying predictions derived from one region to other regions.

CONSISTENCY OF HABITAT RELATIONSHIPS

The potential consistency of habitat relationships across regions is an important parallel conservation question. We found that a similar hierarchy of habitat variables explained the occurrence of koalas in each region, validating the importance of a hierarchical landscape approach to koala conservation across its range. However, like Whittingham *et al.* (2007), who found that patterns of habitat association for farmland birds varied on a regional basis, we found that the effect size and rank of most individual variables within the hierarchy varied regionally for the koala (Table 2). Therefore there is a strong justification for adopting a hierarchical approach to koala conservation across its broad geographical range, but differences in habitat relationships within this hierarchy make a uniform conservation programme misguided.

We found that some site and landscape variables affect the distribution of koalas in similar ways (in terms of effect size, direction of effect and rank) across regions (Table 2). The importance of tree species is attributed to an evolutionary selection by koalas for particular foliar nutrients associated with certain *Eucalyptus* species growing on fertile soils. This preference is the principal determinant of koala distribution and density within their range in the absence of widespread human-induced landscape change. This finding supports previous research that koalas are highly specialized folivores that prefer certain eucalypt species, especially when they

Table 2. Summary of effect size and variable rank for the three study areas

Variable	Noosa		Port Stephens		Ballarat	
Tree scale						
Tree basal area	***/†††	(+)	*/†	(+)	*/††	(+)
Tree species class	***/†††	(+)	**/††	(+)	***/†††	(+)
Tree species : tree basal area	**/††	(+)	*/†	(+)	*/†	(+)
Stand scale						
Soil substrate	*/†	(+)	***/†††	(-)	***/†††	(+)
Proportion of primary tree species	*/†	(+)	*/†	(+)	***/†††	(+)
Patch and landscape scales						
Patch size	*/†	(+)	***/††	(+)	***/††	(+)
Distance-weighted habitat metric	***/†††	(+)	***/†††	(-)	***/††	(+)
Proportion of highly suitable habitat	**/††	(+)	**/††	(+)	*/†	(+)
Road density	**/††	(-)	***/†††	(-)	*/†	(+)

***Effect size >0.3; **effect size 0.1–0.3; *effect size <0.1.

†††Three top-ranked variables; ††three mid-ranked variables; †three lowest-ranked variables.

(+) Positive effect; (-) negative effect.

occur on fertile soils (Phillips, Callaghan & Thompson 2000; Moore & Foley 2005).

Also similar across regions was the importance of landscape context, as indicated by the distance-weighted habitat metric. However the metric had a negative effect for Port Stephens. This is counter-intuitive, as one would expect a higher probability of occurrence in more connected landscapes with more habitat. This difference is explained by several absence sites ($n = 12$) occurring in a block of largely intact, but lower quality, suitable and marginal habitat in the north-west of Port Stephens. As with many forest-dependent wildlife populations (Rochelle, Lehmann & Wisniewski 1999), koala populations have been adversely affected by extensive clearing of their favoured habitat (ANZECC 1998), causing contractions in their distribution and local extinctions. This is consistent with recent studies demonstrating the importance of landscape context for other Australian arboreal marsupials (Lindenmayer *et al.* 1999; McAlpine & Eyre 2002).

Despite some similarities, the effect size and rank of the majority of habitat variables differed across regions (Table 2). The interaction of local edaphic factors, a dominance of less suitable regrowth forests, and a history of local extinctions and translocations add a strong local dimension to the Ballarat study, which differentiates it from the other regions. Koala populations in Ballarat are concentrated in highly suitable habitats occurring on fertile, volcanic-derived substrates. For Port Stephens, the present-day koala distribution is an artefact of historical clearance of koala habitat on inland floodplains (Knott *et al.* 1998) and the current concentration of preferred tree species on sandy soils, rather than the influence of a sandy substrate *per se*. In Noosa, historical clearing has not been as extensive (Seabrook *et al.* 2003), although contemporary habitat loss is affecting koala distributions (McAlpine *et al.* 2006). The effect and rank of roads also varied among regions. For Noosa and Port Stephens, the moderate negative effects and relative importance of roads were indicative of fragmented semi-urban landscapes, subdivided by a network of roads, being unsuitable for koalas. For Ballarat, the weakly positive effect indicates that koala populations may still remain in landscapes fragmented by roads up to the point where road mortality and isolation factors overwhelm the benefits of remnant high-quality habitat.

APPROACH AND LIMITATIONS

The research outcomes depended on developing a hierarchical conceptual model, which integrated multivariate and multicausal factors influencing the occurrence of koalas in fragmented forest landscapes. We found that the mixed-effects models were well suited to analysis of the hierarchically structured landscape data, which included both random and fixed effects. The aim of the analysis was to rank the importance of a set of *a priori* explanatory variables. The information-theoretical approach used to achieve this aim was useful for capturing both model and parameter uncertainty, which were often quite high. The low precision of the lower-ranked parameter estimates reflects their weak effect in the model

and confirms their lower ranking. The low–moderate level of discrimination ability of the models for each region reflects either large and noisy data sets, the possibility that an important explanatory variable was excluded, or that some habitat relationships may be nonlinear (Rhodes *et al.* 2008).

Failure to account for spatial autocorrelation in species distribution models can lead to incorrect conclusions regarding the effect and rank of habitat variables as determinants of species' occurrence. The models for Ballarat and Port Stephens effectively accounted for spatial autocorrelation in the residuals, reflecting the wider spacing of sites and hence their spatial independence. For Noosa, the autocorrelation at the 500-m lag was attributed to a small number of closely adjacent sites, while the evidence of some spatial autocorrelation at the 2- and 5-km lag distances is possibly due to the interaction of movement processes and landscape pattern that are not represented in the model. However, this is unlikely to affect the model performance because the assumption of independent errors was violated at only three out of the 20 lag distances.

SYNTHESIS

Adopting a uniform conservation programme over a large geographical area is attractive to policy-makers and conservation planners. It allows efficiencies in programme development and application. It is tempting to extrapolate species–habitat relationships derived from a single study to other regions. Our findings demonstrate that there is some hope that a similar hierarchy of factors will influence species distributions from region to region, particularly where environmental and land-use characteristics are similar. However, we argue against adopting a uniform conservation programme for species with a large geographical range. A species may experience regional differences in the spatial and historical impact of human land-use pressures on its natural habitat, especially at the patch and landscape scales where human impacts are strongest.

Our findings emphasize the necessity to develop conservation strategies at a hierarchy of multiple spatial scales, while simultaneously taking into account cross-regional differences to manage wildlife populations throughout their range. Unless conservation and planning efforts are effectively coordinated across regions, and priorities recognize the importance of a hierarchy of habitat factors, including landscape context, the long-term prospects for managing koala (and other wildlife) populations will be diminished. We conclude that multiscale models of koala distribution cannot be readily generalized from region to region, and that specific conservation actions for each region, rather than the entire geographical range, are more appropriate.

Acknowledgements

We acknowledge the Australian Research Council (Grant No. C00107594) and the Australian Koala Foundation for funding this study. Many thanks also to the numerous volunteers who assisted with the field surveys. Finally, thanks to Phil Stephens and Fangliang He for their comments on an earlier version of this paper.

References

- ANZECC (1998) *National Koala Conservation Strategy*. Australia and New Zealand Environment and Conservation Council, Environment Australia, Canberra.
- Booth, G.D., Niccolucci, M.J. & Schuster, E.G. (1994) *Identifying Proxy Sets in Multiple Linear Regression: An Aid to Better Coefficient Interpretation*. Research paper INT-470. United States Department of Agriculture, Forest Service, Ogden, UT, USA.
- Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.
- Buckley, Y.M., Briese, D.T. & Rees, M. (2003) Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. *Journal of Applied Ecology*, **40**, 481–493.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.
- DeGraff, R.M. & Rappole, J.H. (1995) *Neotropical Migratory Birds: Natural History, Distribution and Population Change*. Cornell University Press, Ithaca, NY, USA.
- ESRI (2004) *ArcGIS*. Environmental Systems Research Institute, Redlands, CA, USA.
- Fielding, A.H. & Haworth, P.F. (1995) Testing the generality of bird-habitat models. *Conservation Biology*, **9**, 1466–1481.
- Fuhlendorf, S.D., Woodward, A.J.W., Leslie, D.M.J. & Shackford, J.S. (2002) Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landscape Ecology*, **17**, 617–628.
- Gaston, K.J., ed. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford, UK.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Guisan, A., Lehmann, A., Ferrier, S. et al. (2006) Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology*, **43**, 386–392.
- Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, UK.
- Hosmer, D.W. & Lemeshow, S. (2000) *Applied Logistic Regression*, 2nd edn. John Wiley & Sons, New York.
- Knott, T., Lunney, D., Coburn, D. & Callaghan, J. (1998) An ecological history of koala habitat in Port Stephens Shire and the Lower Hunter on the Central Coast of New South Wales, 1801–1998. *Pacific Conservation Biology*, **4**, 354–368.
- Laurance, W.F. & Bierregaarde, R.O. (1997) *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, IL, USA.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd edn. Elsevier, Amsterdam.
- Lindenmayer, D.B., Cunningham, R.S., Pope, M.L. & Donnelly, C.F. (1999) The response of arboreal marsupials to landscape context: a large-scale fragmentation study. *Ecological Applications*, **9**, 594–611.
- Lunney, D., Phillips, S., Callaghan, J. & Coburn, D. (1998) Determining the distribution of koala habitat across a shire as a basis for conservation: a case study of Port Stephens, New South Wales. *Pacific Conservation Biology*, **4**, 186–196.
- Martin, R. & Handasyde, K. (1999) *The Koala: Natural History, Conservation and Management*, 2nd edn. University of New South Wales Press, Sydney.
- Matthews, A., Lunney, D., Gresser, S. & Maitz, W. (2007) Tree use by koalas *Phascolarctos cinereus* after fire in remnant coastal forest. *Wildlife Research*, **34**, 84–93.
- McAlpine, C.A. & Eyre, T.J. (2002) Testing landscape metrics as indicators of habitat loss and fragmentation in continuous eucalypt forests (Queensland, Australia). *Landscape Ecology*, **17**, 711–728.
- McAlpine, C.A., Rhodes, J.R., Callaghan, J. et al. (2006) The importance of forest area and configuration relative to local habitat factors for conserving forest mammals: a case study of koalas in Queensland, Australia. *Biological Conservation*, **132**, 153–165.
- McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2004) *FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps*. Computer software program produced by the authors, University of Massachusetts, Amherst, MA, USA.
- McKay, M., Beckman, R. & Conover, W. (1979) Comparison of three methods for selecting values of input variables in the analysis of output from computer code. *Technometrics*, **21**, 239–245.
- Moore, B.D. & Foley, W.J. (2005) Tree use by koalas in a chemically complex landscape. *Nature*, **435**, 488–490.
- Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.
- Pearson, S.M., Turner, M.G., Gardner, R.H. & O'Neill, R.V. (1996) An organism perspective of habitat fragmentation. *Biodiversity in Managed Landscapes: Theory and Practice* (eds R.C. Szaro & D.W. Johnston), pp. 77–95. Oxford University Press, New York.
- Phillips, S., Callaghan, J. & Thompson, V. (2000) The tree species preferences of koalas (*Phascolarctos cinereus*) inhabiting forest and woodland communities on Quaternary deposits in the Port Stephens area, New South Wales. *Wildlife Research*, **27**, 1–10.
- Pinheiro, J.C. & Bates, D.B. (2000) *Mixed-Effects Models in s and s-PLUS*. Springer, New York.
- Rhodes, J.R., McAlpine, C.A., Lunney, D. & Possingham, H.P. (2005) A spatially explicit habitat selection model incorporating home range behavior. *Ecology*, **86**, 1199–1205.
- Rhodes, J.R., Wiegand, T., McAlpine, C.A. et al. (2006) Modelling species distributions for improving conservation in semi-urban landscapes: a koala case study. *Conservation Biology*, **20**, 449–459.
- Rhodes, J.R., Callaghan, J.G., McAlpine, C.A., de Jong, C., Bowen, M.E., Mitchell, D.L., Lunney, D. & Possingham, H.P. (2008) Regional variation in habitat-occupancy thresholds: a warning for conservation planning. *Journal of Applied Ecology*, **45**, doi: 10.1111/j.1365-2664.2007.01407.x.
- Rochelle, J.A., Lehmann, L.A. & Wisniewski, J. (eds) (1999) *Forest Fragmentation: Wildlife and Management Implications*. Brill, Leiden, the Netherlands.
- Rushton, S.P., Ormerod, S.J. & Kerby, G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology*, **41**, 193–200.
- Saab, V. (1999) Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications*, **9**, 135–151.
- Sawada, M. (1999) ROOKCASE: an EXCEL 97/2000 VISUAL BASIC (VB) add-in for exploring global and local spatial autocorrelation. *Bulletin of the Ecological Society of America*, **80**, 231–234.
- Seabrook, L.M., McAlpine, C.A., Phinn, S.R., Callaghan, J. & Mitchell, D. (2003) Landscape legacies: koala habitat change in Noosa Shire, south-east Queensland. *Australian Zoologist*, **32**, 446–261.
- Vaida, F. & Blanchard, S. (2005) Conditional Akaike information for mixed-effects models. *Biometrika*, **92**, 351–370.
- Vanreusel, W., Maes, D. & Van Dyck, H. (2006) Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation Biology*, **21**, 201–212.
- Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D. & Freckleton, R.P. (2007) Should conservation strategies consider spatial generality: farmland birds show regional not national patterns of habitat association? *Ecology Letters*, **10**, 25–35.
- Wiens, J.A. (1997) The emerging role of patchiness in conservation biology. *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity* (eds S.T.A. Pickett, R. S. Ostfeld, M. Shachak & G.E. Likens), pp. 93–107. Chapman & Hall, New York.

Received 13 December 2006; accepted 14 September 2007

Handling Editor: Fangliang He

Supplementary material

The following supplementary material is available for this article.

Table S1. Tree species used by koalas for each study region.

Table S2. Explanatory variables at each scale of analysis.

Fig. S1. Koala utilization of tree preference categories by study region.

Fig. S2. Correlogram of average model residuals by study region.

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