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The importance of forest area and configuration relative to local habitat factors for conserving forest mammals: A case study of koalas in Queensland, Australia

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ABSTRACT

The loss and fragmentation of forest habitats by human land use are recognised as important factors influencing the decline of forest-dependent fauna. Mammal species that are dependent upon forest habitats are particularly sensitive to habitat loss and fragmentation because they have highly specific habitat requirements, and in many cases have limited ability to move through and utilise the land use matrix. We addressed this problem using a case study of the koala (*Phascolarctos cinereus*) surveyed in a fragmented rural–urban landscape in southeast Queensland, Australia. We applied a logistic modelling and hierarchical partitioning analysis to determine the importance of forest area and its configuration relative to site (local) and patch-level habitat variables. After taking into account spatial autocorrelation and the year of survey, we found koala occurrence increased with the area of all forest habitats, habitat patch size and the proportion of primary *Eucalyptus* tree species; and decreased with mean nearest neighbour distance between forest patches, the density of forest patches, and the density of sealed roads. The difference between the effect of habitat area and configuration was not as strong as theory predicts, with the configuration of remnant forest becoming increasingly important as the area of forest habitat declines. We conclude that the area of forest, its configuration across the landscape, as well as the land use matrix, are important determinants of koala occurrence, and that habitat configuration should not be overlooked in the conservation of forest-dependent mammals, such as the koala. We highlight the implications of these findings for koala conservation.

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1. Introduction

The conservation of forest mammals, as exemplified by the koala (*Phascolarctos cinereus*), depends upon understanding

its ecology in the context of the multiple threats facing forests that are commercially valuable both as timber, as well as for other land uses, such as agriculture, urban areas and roads. The loss and fragmentation of forest habitats by human land

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use are recognised as important factors influencing the decline of forest-dependent fauna (e.g., McAlpine and Eyre, 2002; McGarigal and McComb, 1995; Rochelle et al., 1999). The loss of forests results in a reduction in the area of forest habitat, and fragmentation is the process by which forest habitat is broken apart, independent of pure habitat loss (Fahrig, 1997, 1999, 2003).

Some mammal species that depend upon forest habitats are particularly sensitive to habitat loss and fragmentation (Newell, 1999; Lindenmayer et al., 2000; McAlpine and Eyre, 2002). They are often characterised by highly specific habitat requirements and limited movement capabilities through the land use matrix (Lindenmayer et al., 1990; Incoll et al., 2001). An inability to utilise the matrix makes them particularly vulnerable to the effects of habitat loss and fragmentation (Laurance, 1990, 1991, 1994). Many forest-dependent mammal species (other than bats) also cannot cross, or are reluctant to cross, large areas of cleared land (Bakker and Van Vuren, 2004; van der Ree et al., 2004). Even where individuals do cross cleared areas, they are commonly subjected to elevated mortality due to factors such as predation and vehicle collisions (Goosem, 2004; van der Ree et al., 2004). Hence, the effects of isolation can increase rapidly as forest habitat is fragmented. These factors mean that it is important to understand the implications of habitat loss and fragmentation for forest-dependent mammal species, particularly where human populations continue to clear and fragment forest landscapes.

The koala provides an ideal case study for testing the relative importance of forest area and configuration relative to local (<1 ha) habitat quality. The majority of koala research has focused on habitat quality at the level of the individual tree or vegetation community (e.g., Degabriele, 1983; Cork et al., 1990; Phillips and Callaghan, 2000; Ellis et al., 2002; Moore et al., 2004a,b; Moore and Foley, 2005). Central to these studies is the hypothesis that the distribution of koalas is determined by the distribution of the more nutrient-rich foliage of preferred eucalypt species, especially when these trees occur on more fertile soils (Moore et al., 2004a). However, the effect of forest loss and configuration relative to these fine-scale habitat factors has not been tested. This is an important limitation because the koala has experienced population declines and local extinctions across its geographic range. The major underlying cause of koala decline is clearing of eucalypt forests for agricultural development of inland regions and continuing growth of the human population along the forested eastern coastal fringe (ANZECC, 1998; Melzer and Houston, 2001; Reed and Lunney, 1990). Rhodes et al. (2006) found that habitat area and anthropogenic variables, such as roads and dogs, are important for determining the distribution of koalas in the Port Stephens Shire (coastal New South Wales), but their effects vary spatially according to land use.

Koalas are considered to be sensitive to forest fragmentation, with much of their remaining high quality habitat now fragmented, and surrounded by urban and agricultural land use (Knott et al., 1998; Seabrook et al., 2003). Koalas can move from tree to tree where canopies overlap, but frequently come to the ground to cross non-forest gaps, including cleared land between individual patches of trees (Dique et al., 2003; Lunney et al., 2002; Rhodes et al., 2006). However, to cross gaps,

the risk of mortality is much higher. In semi-urban landscapes, roads subdivide habitat, acting as barriers to koala movement, with road deaths recognised as a major source of koala mortality in fragmented urban landscapes (Lunney et al., in press). Dogs also gain a predatory advantage when the koala is forced to travel across open ground, such as when crossing a road or cleared areas.

This study addressed the question: how important are forest area and configuration relative to fine-scale habitat variables, such as tree species, for the occurrence of koalas in a fragmented rural–urban landscape of coastal Southeast Queensland (Australia)? We applied a logistic modelling and hierarchical partitioning approach to test the relative importance of forest area, configuration and roads at the landscape-level (100–1000 s ha), patch-size at the patch-level (1–100 s ha), and soil–substrate and the proportion of primary tree species at the local or site-level, plus the effect of spatial autocorrelation between neighbouring koala survey sites. We show that forest area, forest configuration, and roads at the landscape-level, and the proportion of primary tree species at the site-level, all have strong independent effects on the occurrence of koalas, with the proportion of primary tree species, road density, forest area, and forest mean nearest neighbour distance being the most important predictors.

1.1. Study species

The tree is the basic unit of survival for koalas. It has long been recognised that koalas demonstrate marked preferences for a relatively small number of the *Eucalyptus* species in any area (e.g., Phillips and Callaghan, 2000; Phillips et al., 2000; Ellis et al., 2002; Braithwaite, 2004; Moore et al., 2004a,b, 2005; Smith, 2004). Therefore, koala habitat generally consists of forest associations containing the preferred *Eucalyptus* tree species, although other factors, such as tree size, can also contribute to habitat quality (Smith, 2004). Koalas occupy home ranges, which vary widely between populations, and can range from as little as 3 ha in high quality coastal habitats to over 200 ha in semi-arid inland habitats. Although largely solitary animals, the home ranges of males and females generally overlap (Dique et al., 2003). Dispersal occurs at around 1–2 years of age, with dispersal distances of over 10 km being recorded.

2. Methods

2.1. Study area

The Study area was Noosa Shire (26.50S, 152.50E; 86,823 ha) in coastal southeast Queensland, Australia (Fig. 1). The climate is sub-tropical with vegetation communities ranging from coastal heaths on Pleistocene sand deposits to sub-tropical rainforests and wet eucalypt forests on granite intrusions and volcanic soils, and dry eucalypt forests on alluvium and sandstones (Thompson, 1975). Urban land use is dominant in the coastal southeast, with a mixture of low-density rural-residential and rural land use in the elevated western areas. Much of the remaining, relatively intact koala habitat occurs in State Forests (timber reserves) and National Parks, although the latter are concentrated on infertile sandy soils in the northeast of

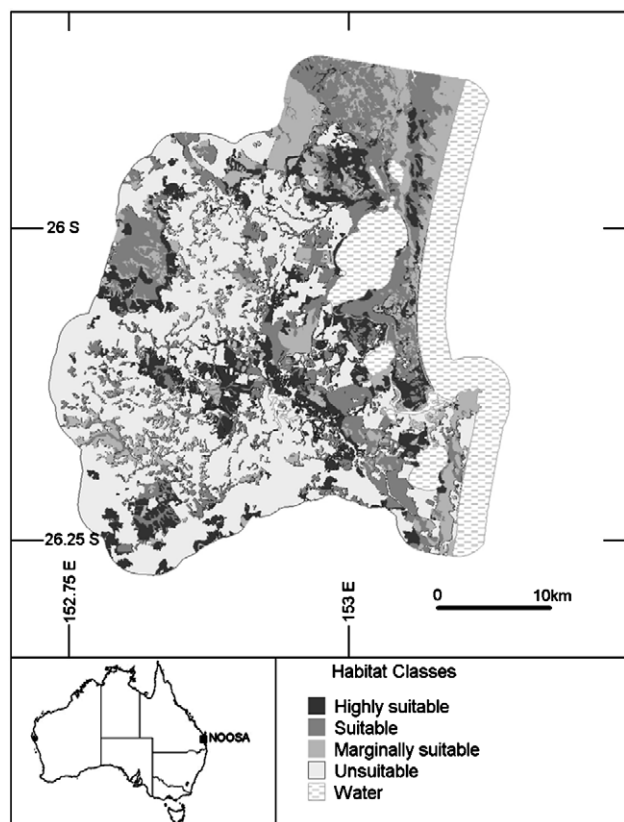


Fig. 1 – Location of the Noosa Shire study area showing the distribution of the koala habitat quality classes. A description of the habitat classes is provided in Table 1.

the study area where koala habitat suitability is generally low. Present-day landscapes are a legacy of European settlement dating back to 1860, with over 50% of koala habitat cleared (Seabrook et al., 2003). Habitat loss accelerated from 1890 to 1910, when the area of farmland grew to over 45,000 ha, mainly for dairy farming on fertile soils in the west. After a period of relative stability between 1940 and 1960, a further 35% of the remaining habitat was lost, mainly in the southeast as a result of rapid coastal urbanization, driven by growth of the tourist industry since 1970.

2.2. Habitat suitability classes

We combined six habitat categories from the Noosa Koala Habitat Atlas (scale 1:25,000) prepared by the Australian Koala

Foundation (<http://www.savethekoala.com/maps.html>) into four habitat suitability classes: highly suitable, suitable, marginal and unsuitable (Table 1). We converted these classes into a raster grid (grid size 25 m) using ArcGIS (ESRI, 2004). The Koala Habitat Atlas was based primarily on vegetation communities interpreted from aerial photographs. The habitat suitability class for each vegetation community was assigned using the proportional abundance of the identified preferred (i.e. primary and secondary) food tree species (Callaghan, Thompson, Bowen and Mitchell unpublished data). A primary koala food tree is a *Eucalyptus* species with a significantly higher proportion of surveyed trees having one or more koala faecal pellets compared to other tree species. The presence of the distinctive faecal pellets of koalas, located around the base of trees, is routinely used as an indicator of use (Phillips and Callaghan, 2000; Phillips et al., 2000). Similarly, a secondary food tree is principally a *Eucalyptus* species that registers a significantly higher proportion of trees with faecal pellets compared to that observed for remaining species (excluding the primary category). A third category, supplementary food tree species, record a significantly lower proportion of pellets than for secondary species, but greater than for other tree species that generally lack evidence of use by koalas. It is also acknowledged that non-eucalypt species often provide supplementary food resources for koalas, whilst eucalypt and non-eucalypt species collectively provide crucial shelter resources.

2.3. Koala surveys

Three surveys of koala occurrence, conducted using similar methods at different times, were combined into a single large data set ($n = 352$) to increase the power of the analysis. The first survey ($n = 70$) was an assessment of koala distribution in Noosa Shire conducted by the Australian Koala Foundation in 1997 in rural landscapes in the west of the study area. Historical aerial photographs show that these rural landscapes experienced minimal clearing since 1990. The second survey ($n = 100$) was conducted in winter 2001, while the third survey ($n = 182$) was conducted in winter–spring 2002. Sites for the 2001–2002 surveys were selected according to a combination of a random stratified and Latin hypercube design (McKay et al., 1979; Thompson, 1992). Patch habitat quality was the key categorical variable, while habitat patch size, distance to sealed roads and the proximity to neighbouring habitat patches of similar quality were continuous variables. Sampling focused on the highly suitable and suitable habitat

Table 1 – Habitat classes derived for this study from the Australian Koala Foundation’s Habitat Atlas classification				
Habitat class	Proportion of overstorey tree species			Function
	Primary eucalypt species	Primary and secondary eucalypt species	Secondary eucalypt species	
Highly suitable	≥ 30%	or ≥ 50%	or ≥ 50%	High quality breeding, low risk movement
Suitable	10 < 30%	or 30 < 50%	or 10 < 50%	Breeding, low risk movement
Marginal	< 10%	or < 30%	or < 10%	Low quality breeding, low risk movement
Unsuitable	Scattered trees	Scattered trees	Scattered trees	High risk movement

classes, with larger habitat patches sampled multiple times to take into account internal variation in habitat quality and resource use by koalas. We endeavoured to locate sites a minimum of 750 m apart, although approximately 30% of sites were within 500 m of a neighbouring site due to the different survey dates and logistical constraints, thereby increasing the problem of spatial dependence.

Obtaining occurrence and abundance estimates for koalas, over broad areas, is notoriously difficult due to their cryptic nature and because they often occur at low densities. For this reason, the presence/absence of koala faecal pellets in a site was the preferred survey method for detecting koala presence/absence. The particular advantage of searching for koala pellets is that pellet shape and other characteristics are species-specific, aiding identification, pellets persist after a koala has departed, and are easy to find. This method has the ability to determine koala distribution over 10,000–100,000 s ha within a relatively short time. Limitations of pellet surveys include (i) general inability to determine numbers of individual koalas, and (ii) differential pellet decay rates over time and space. Lunney, Rhodes, Moon, Matthews and McAlpine (unpublished data) showed that average decay rates of koala faecal pellets for Port Stephens Shire (a region with similar annual rainfall and habitats to Noosa) were relatively slow, depended upon rainfall and varied between locations. They conclude that this field technique is sound, particularly when only presence/absence is the measure used, but differences in decay rates are relevant limitations for any studies that rely on finding pellets. Given the below average rainfall prior to the 2001–2002 survey times, we are confident the method had a low observation error.

Pellet searches were undertaken at each site according to the methods in Phillips and Callaghan (2000) and Phillips et al. (2000). Once the site location was determined, a suitable tree (preferably a primary food tree) was selected to mark the centre of the plot. The search consisted of the centre tree, and the next closest trees, with a minimum diameter at breast height of 10 cm. A minimum of 30 trees and a maximum of 36 trees were surveyed for each site. A catchment consisting of a 1-m wide strip around the base of each tree was searched for up to two-person minutes, unless a koala pellet was found within that period. A presence was recorded for each site where one or more koala pellets were found.

2.4. Spatial autocorrelation

Failure to account for spatial autocorrelation in species–environment relationships can lead to incorrect conclusions regarding the absolute and relative importance of environmental variables as determinants of species occurrence or abundance (White and Engelen, 1997). To account for spatial autocorrelation in the koala presence/absence data, we first tested for spatial autocorrelation at 500 m distance intervals within an 8 km neighbourhood using Moran's Index calculated in ArcGIS, and then plotted the output as a correlogram. The correlogram showed that strongest spatial autocorrelation occurred within a 500 m neighbourhood, with a gradual decline with neighbourhood distance (Fig. 2a). Hence, we then incorporated the effect of this spatial autocorrelation as a term in the regression model (Keitt et al., 2002). This effect

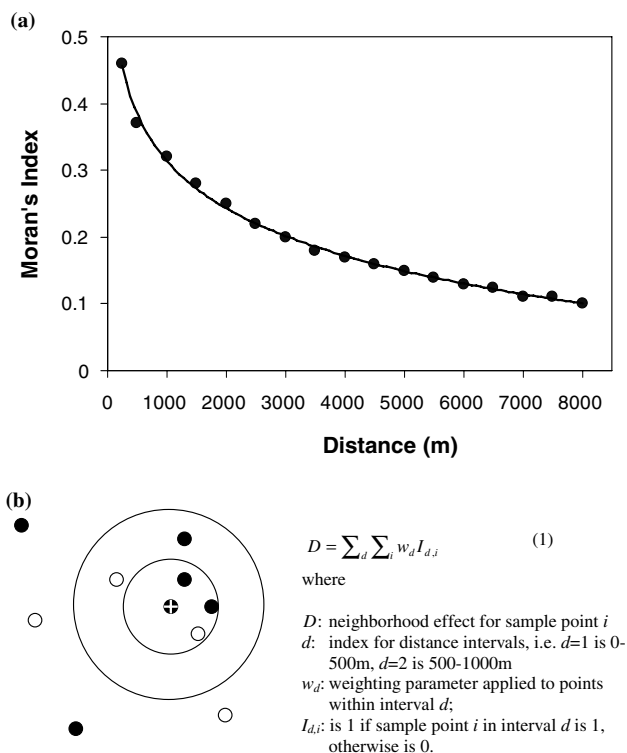


Fig. 2 – (a) Correlogram showing decline in spatial autocorrelation as measured by Moran's Index with increased size of the neighbourhood around each survey site. (b) Neighbourhood effect as an indicator for co-occurrence of the koala's presence for sample points. Black dots represent sites where koala pellets were present, white dots where pellets were absent.

was derived by counting the number of presence sites around a sample point within 0–500 and 500–1000 m distance intervals, weighted to account for area density and the degree of interactions occurring within each distance interval (Fig. 2b; Eq. (1)). Statistical analysis confirmed that, at distances >1000 m, the likelihood of co-occurrence of koala presence was the same as for the whole region, and within 500 m it was three times more likely than within the 500–1000 m interval. The 0–500 m relationship was subsequently used to define the weighting parameter for the spatial autocorrelation term (D).

2.5. Explanatory variables

Trees of all species with a diameter ≥ 10 cm were recorded at each site (Table 2), and subsequently grouped as primary, secondary, supplementary or other (not utilised) categories. Soil classes were derived from geology mapping of southeast Queensland at a scale of 1:100,000. The 81 different lithology units mapped for Noosa Shire were assigned into four broad, ordinaly ranked, soil classes: sand, sandy loam, clay loam, and clay (Table 2).

The focal patch size of each habitat quality class, referred to as habitat patch size, was calculated for each survey site by intersecting the site location with the Koala Habitat Atlas polygons using ArcGIS. In largely intact landscapes, it is a

Table 2 – Description of explanatory variables used to predict Koala presence–absence

Variable	Units	Full description
<i>Site-level</i>		
Proportion of primary food trees	Percent	Proportion of primary food trees present at a study site (field measured variable)
Soil type	Categorical	Soil type ordinaly ranked into the following categories. 1 = sand, 2 = sandy loam, 3 = clay loam, 4 = clay
<i>Patch-level</i>		
Habitat type	Categorical	Habitat types ordinaly ranked according to the proportion of food trees (Table 1). 1 = highly suitable, 2 = suitable, 3 = marginal, 4 = unsuitable
Habitat patch size	Hectares	Habitat patch size (ha)
Perimeter:area ratio of focal patch	Ratio	Patch perimeter (m) divided by patch area (m ²) (McGarigal and Ene, 2003)
Habitat mean proximity index	None	A habitat mean proximity index which measures inverse distance from neighbouring patches taking into account habitat quality and patch isolation
<i>Landscape-level</i>		
Proportion of habitat class in the landscape	Percent	The percentage of the landscape occupied by: highly suitable habitat; suitable habitat; marginal habitat; highly suitable and suitable habitats combined, and highly suitable, suitable and marginal habitats combined
Forest patch density	Patches/100 ha	Density of total forest patches in the landscape
Forest mean nearest neighbour distance	Meters	Euclidean mean nearest neighbour distance (m) between neighbouring forest patches within a maximum search radius of 3000 m (McGarigal and Ene, 2003)
Density of sealed roads	Meters/hectare	Total length of sealed roads (m) divided by the landscape area (ha)
Distance to sealed roads	Meters	Euclidean distance of site to nearest sealed road
D	Ratio	Spatial autocorrelation term (White and Engelen, 1997)
Year	Year	Year of survey date

measure of the natural heterogeneity in forest composition, while in fragmented landscapes, patch size also indicates loss of habitat for agricultural and urban land use. The external boundary of the habitat map was extended by 5 km to account for adjoining habitat patches in neighbouring shires. The perimeter:area ratio for each focal patch was calculated according to McGarigal and Ene (2003). FRAGSTATS Version 3 (McGarigal et al., 2004) was used to quantify the proportion of suitable habitat (not including water bodies) at five radial extents (1, 2, 3, 4 and 5 km) from each survey site (Table 1). This metric was calculated for: (i) highly suitable; (ii) suitable; (iii) highly suitable + suitable; and (iv) highly suitable + suitable + marginal habitat. Testing for the effect of habitat configuration was undertaken using the merged highly suitable, suitable and marginal habitat classes (hereafter referred to as forest habitat). FRAGSTATS was then used to quantify the density of forest patches, referred to as forest patch density, for each radial extent. To test for the effect of habitat proximity, the mean Euclidean nearest neighbour distance between forest patches was calculated for the five radial extents. The density of sealed roads within each of the five radial extents was calculated using ArcGIS.

2.6. Statistical analyses

Statistical analyses were performed using the R public-domain statistical package (R Project for Statistical Computing

release 1.9.0 <http://www.r-project.org>). An assessment for normality showed many of the data had a skewed distribution. A $\sqrt{(x+1)}$ transformation was subsequently applied to correct for this skewed distribution. Explanatory variables were standardised to have a mean of 0 and a standard deviation 1 to allow comparison of model parameter estimates. Spearman's rank correlation was applied to test for collinearity between variables at each level. Booth et al. (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.

First, we modelled the probability of koala presence for each explanatory variable, including the spatial autocorrelation term *D* and year, using univariate logistic regression (Hosmer and Lemeshow, 2000). We compared univariate models using Akaike's Information Criterion (AIC) (Akaike, 1983). We calculated AIC as

$$AIC = -2L + 2K \quad (2)$$

where *L* is the log-likelihood of the model and *K* is the number of parameters in the model. For habitat area, forest patch density, forest mean nearest neighbour distance, and road density, we chose the spatial extent within each variable with the highest Akaike weight value (Akaike, 1983; Burnham and Anderson, 2002). The Akaike weight (w_i) of a model is the relative likelihood of the model compared to all other models in the set with

weight values >0.9, indicating a high level of support for a candidate model (Burnham and Anderson, 2002). To test for how the effect of forest area, configuration and road density changed with the spatial extent of analysis, we plotted the Akaike weight against the metric mean and standard deviation for each spatial extent, and examined if the Akaike weight followed a similar pattern to the mean and standard deviation. We also tested for statistically important interaction effects between habitat area and forest patch density, and between forest area and forest mean nearest neighbour distance.

Inferences in multiple regression are usually conditional on the selected model; that is, we assume that the model is correct (Buckland et al., 1997). It is more defensible to recognise the uncertainty in model selection when quantifying the precision of a model parameter. For this reason, we applied a model averaging approach to account for model uncertainty (Burnham and Anderson, 2002). First, we reduced the number of model variables to a manageable subset of nine by ranking the univariate models of the explanatory variables and the interactions according to their AICs. We recognised that a potential problem with this approach is that two variables might appear unimportant in separate univariate models, but together may produce a highly parsimonious model. To address this problem, we also checked the combined effect of combinations of excluded variables in multivariate models.

We constructed a set of alternative models from all linear combinations (*number of models* = 512) of the subset of explanatory variables and interactions. The general form of the multivariate logistic regression models was

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_m D + \beta_n \text{Year} \quad (3)$$

where p is the probability of a koala pellet presence; $\beta_0 + \beta_1 X_1 + \dots$ are the linear predictors; $\beta_m D$ is the term for neighbourhood effect D ; $\beta_n \text{Year}$ is the year of the survey.

We then ranked these models by their AIC values and calculated the Akaike weight for each model. To test the goodness-of-fit of the best approximating model, that is the model with the lowest AIC, we applied the Pearson χ^2 (using a normal approximation) and the Hosmer-Lemeshow (\hat{C}) goodness of fit tests (Hosmer and Lemeshow, 2000). We also tested for spatial autocorrelation in the Pearson residuals of the best approximating model using Moran's Index calculated in ArcGIS.

We calculated the model average parameter estimates, and the unconditional standard error of each estimate, from model combinations where the parameters were present according to Burnham and Anderson (2002).

To determine the independent effect of the key explanatory variables and interactions, we ranked the effect size of explanatory variables using hierarchical partitioning analysis using the R-package "hier.part" (Mac Nally and Walsh, 2004). 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; Mac Nally, 2000). The joint effect measures collinearity between model variables. Highly collinear variables have a large joint effect in relation to their independent effects.

Finally, we ranked the variables according to their relative importance by summing the Akaike weight ($\sum w_i$) from all

model combinations where the variable occurred. The larger the sum of the weight value, the more important the variable is relative to the other variables.

3. Results

3.1. Spatial extents of landscape influence

Of the sites surveyed, koala pellets were present in 202 sites and absent from 150 sites. There was no single spatial extent at which key landscape metrics had the strongest effect on the presence/absence of koalas, as identified by their pellets. Similarly, the spatial variation in the mean and standard deviation of the metric values was not correlated with the Akaike weight values of the single-variable logistic regression models for the five spatial extents (Fig. 3). For the univariate models, there was a high level of support for the proportion of the landscape occupied by forest habitat ($w_i = 0.965$; Fig. 3a) and the density of sealed roads ($w_i = 0.995$; Fig. 3c) at the 1 km spatial extent. The 1 and 2 km spatial extents showed the strongest effect for the density of forest patches (Fig. 3b), while the 4 km extent had a high level of support ($w_i = 0.800$) for the mean nearest neighbour distance between forest patches (Fig. 3c).

3.2. Subset of explanatory variables

Overall, there was a low to moderate level of collinearity between the explanatory variables (Table 3). Variables showing the highest level of collinearity included habitat patch size and perimeter:area ratio ($r = -0.74$); the habitat mean proximity index with the proportion of the landscape occupied by highly suitable and suitable habitat combined ($r = 0.62$), and with the mean nearest neighbour distance at the 4 km spatial extent ($r = 0.55$); the proportion of forest habitat at the 1 km spatial extent with the proportion of highly suitable and suitable habitat combined at the 1 km extent ($r = 0.88$), and with forest patch density at the 2 km extent ($r = -0.62$); and distance to sealed roads with road density at the 1 km extent ($r = -0.55$). The spatial autocorrelation term D showed a low to moderate level of correlation with the habitat and landscape variables. The perimeter:area ratio, the habitat mean proximity index, and the distance to sealed roads were subsequently excluded from further analysis.

After taking into account these collinearities, and the AIC values of the univariate models, the final subset of explanatory variables consisted of the proportion of primary tree species, habitat patch size, proportion of forest habitat (1 km extent), forest patch density (2 km extent), forest mean nearest neighbour distance (4 km extent), road density, the interaction of the proportion of forest habitat and forest mean nearest neighbour distance, the spatial autocorrelation term, and the year of the survey.

3.3. Effect of explanatory variables

The model combinations revealed a high level of model uncertainty, with 62 models in the 95% confidence set ($\sum w_i = 0.95$). There was also a high level of parameter uncertainty for several variables (Fig. 4a). The spatial autocorrela-

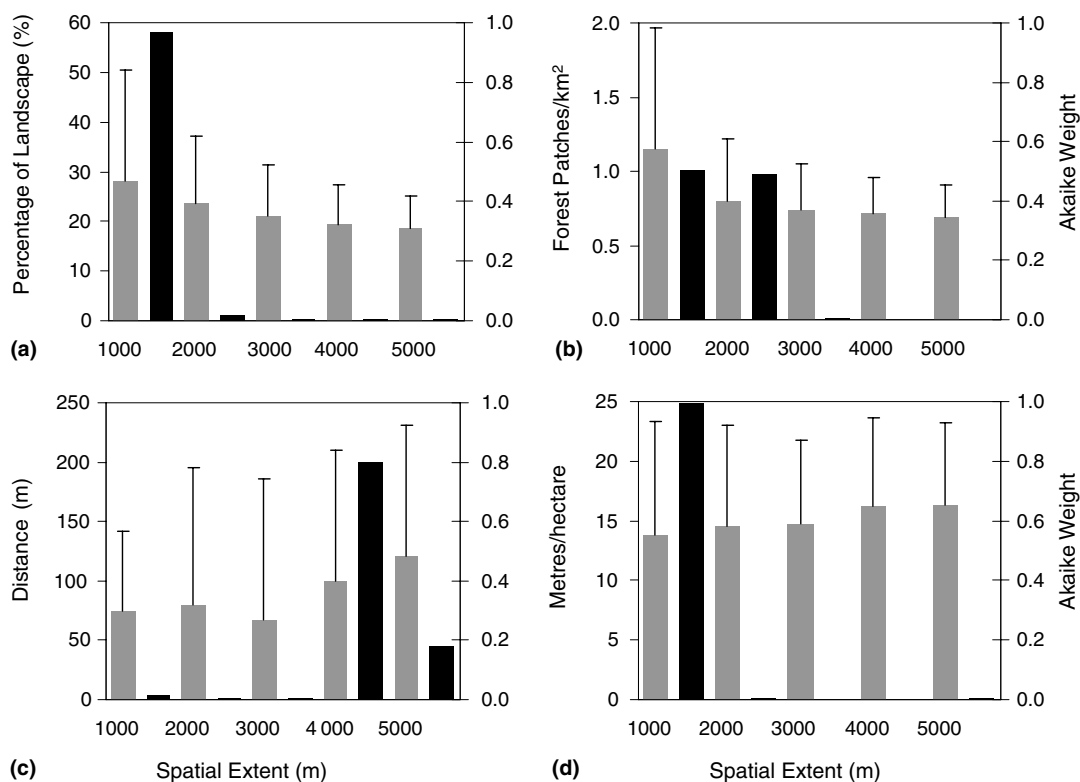


Fig. 3 – Mean (grey shading), standard deviation (error bars) and Akaike weights (w_i) (black shading) of key landscape-scale predictors at increasing spatial extents from koala survey sites. (a) forest habitat as proportion of the landscape; (b) forest patch density; (c) mean nearest neighbour distance; and (d) road density.

Table 3 – Correlation matrix showing Spearman’s rank correlation coefficients for key explanatory variables

Variable	1	2	3	4	5	6	7	8	9	10	11	12
1 Primary tree species	1.00											
2 Patch size	0.06	1										
3 Perimeter:area ratio	-0.08	-0.74	1									
4 Habitat mean proximity index	-0.11	0.38	-0.37	1								
5 Highly suitable habitat (1 km)	-0.05	0.20	-0.25	0.42	1							
6 Highly suitable + suitable habitat (1 km)	-0.01	0.39	-0.40	0.62	0.59	1						
7 Forest habitat (1 km)	0.02	0.34	-0.36	0.49	0.49	0.88	1					
8 Distance sealed roads	0.04	0.07	-0.09	0.11	0.08	0.20	0.33	1				
9 Road density (1 km)	-0.07	-0.12	0.07	-0.05	-0.19	-0.30	-0.40	-0.55	1			
10 Forest patch density (2 km)	0.00	-0.17	0.11	-0.24	-0.25	-0.50	-0.62	-0.33	0.45	1		
11 Mean nearest neighbour (4 km)	0.03	-0.09	0.16	-0.55	-0.22	-0.32	-0.27	-0.03	-0.11	0.16	1	
12 Spatial autocorrelation term (D)	0.04	0.17	-0.28	0.43	0.23	0.34	0.34	0.15	-0.10	-0.17	-0.29	1

Correlated variables with $r \geq \pm 0.50$ are bold.

tion term, followed by the proportion of forest habitat (1 km extent) and the proportion of primary tree species, had the strongest positive effect on koala occurrence. The proportion of the landscape occupied by forest habitat had considerable parameter uncertainty ($\beta = 0.65 \pm 0.71$), reflecting the high level of variability in its effect across all model combinations. Habitat patch size had a moderately positive effect, while forest patch density, mean nearest neighbour distance and road density all had moderate negative effects on the probability of koala occurrence. The year of survey had a weak

positive effect. There was a weak positive interaction between the area of forest habitat and forest nearest neighbour distance. This is explained by: (i) the effect of decreasing the area of forest habitat is stronger on koalas when the neighbouring forest patches are far apart than when they are close, and (ii) the effect of increasing the nearest neighbour distance is less negative on koalas when the area of forest habitat is high.

The best approximating single model contained all variables except for forest patch density. The Hosmer and

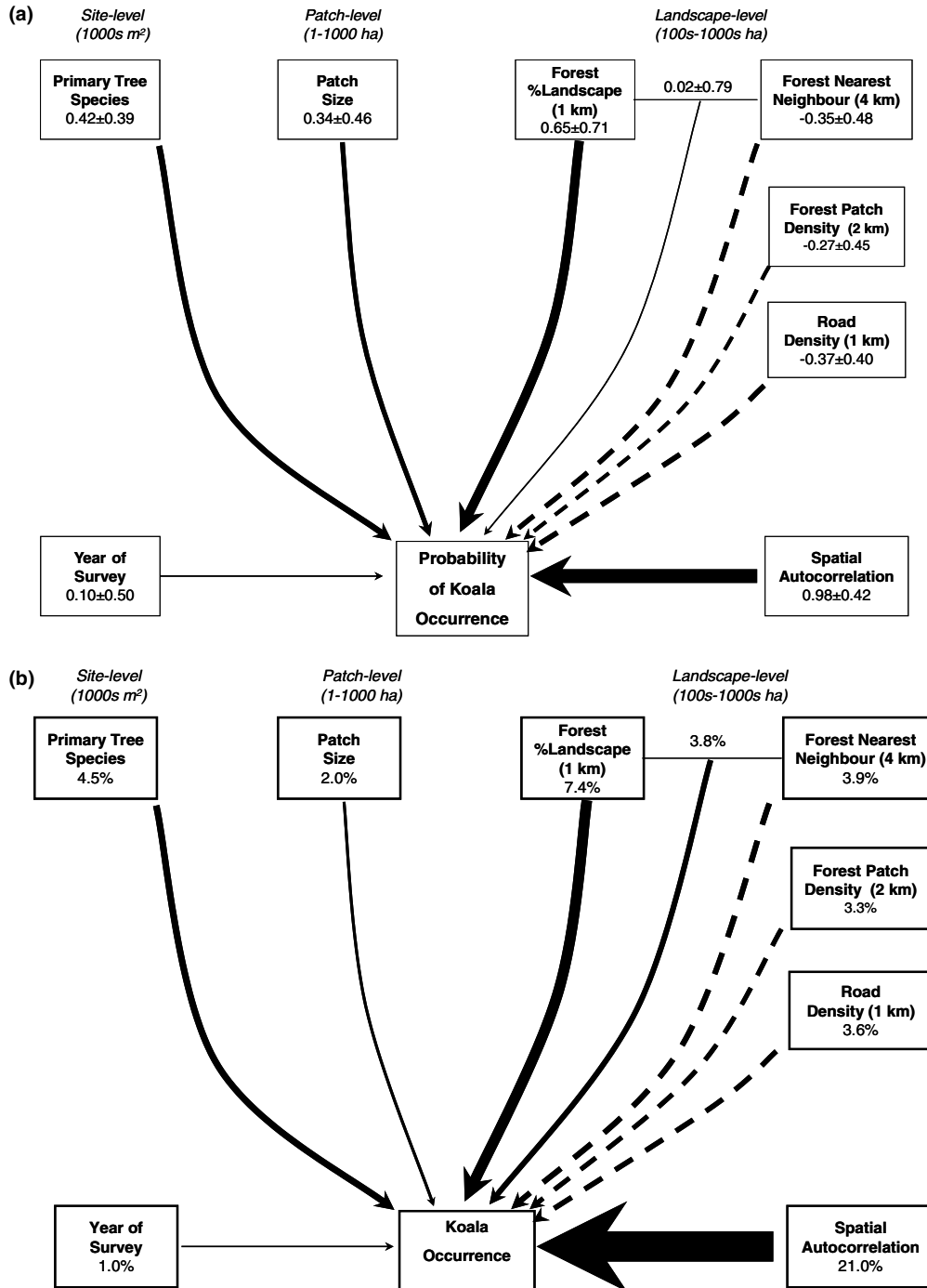


Fig. 4 – Path diagrams showing: (a) the average parameter estimate and the standard error of these estimates for key explanatory variables derived from all combinations of the logistic regression models where the variable was present ($n = 512$); and (b) the independent effect of the key explanatory variables at each level on koala occurrence observed at the site-level. For both diagrams, dashed lines indicate a negative effect, while line width is weighted by the average parameter estimate for (a), and the independent effect size for (b). The line connecting forest %landscape (1 km) and forest nearest neighbour (4 km) represents the interaction effect between these variables.

Lemeshow goodness of fit statistic ($\hat{C} = 0.174$, p value = 0.174) and the Pearson χ^2 statistic ($\chi^2 = 0.154$, p value = 0.877), both indicated good model fit. The residuals of this model were randomly distributed (Moran's $I \sim 0.00$, Z score 0.1) for all spatial neighbourhoods, indicating low unexplained spatial autocorrelation of residuals.

3.4. Independent effect of explanatory variables

The combined, independent effect of the key explanatory variables accounted for 52% of the total explained variation, with a 48% combined joint effect, reflecting the moderate to high level of colinearity between variables (Fig. 4b). The spa-

tial autocorrelation term *D* had a strong independent (21%) and joint effect (10.7%). The proportion of the landscape occupied by forest habitat had the strongest independent effect (7.5%) of the habitat and landscape variables, with the proportion of primary tree species having the next strongest independent effect (4.5%). The forest mean nearest neighbour distance accounted for more of the variance than forest patch density, with the combined independent effect of these measures of landscape configuration accounting for ~7% of the predicted variation. The interaction of forest habitat with the mean nearest neighbour distance accounted for 3.7% of the explained variance. Road density accounted for 3.6% of the explained model variance, making a combined independent effect of ~10.6% for landscape configuration and roads.

3.5. Ranking of explanatory variables

The sum of the Akaike weights showed a ranking pattern (Fig. 5) somewhat different from the independent effect of the hierarchical partitioning analysis (Fig. 4b). This reflects the fact that the Akaike weights do not partition out the independent effect, but rather provide an overall measure of the importance of the variable in explaining the data. The spatial autocorrelation term *D* had the highest Akaike weight (0.995), while the year of survey also had a relatively high weight value (0.882) although its effect size was relatively small (Fig. 4a and b). The proportion of forest habitat had a relatively low weight (0.636) compared to the proportion of primary tree species at the site-level (0.990) and road density (0.899). Forest mean nearest neighbour distance (0.631) and forest patch density (0.439) had a lower rank than the area of forest habitat. The interaction of the proportion of forest habitat and the forest mean nearest neighbour distance had a low Akaike weight (0.360).

4. Discussion

4.1. Model uncertainty

The primary aim of this study was to test the importance of both forest area and its configuration for the conservation of a forest mammal, the koala, in a fragmented, rural–urban landscape of Southeast Queensland, Australia. Inferences drawn from the modelling results are conditional on the high level of model uncertainty and lack of precision in the parameter estimates. However, as Buckland et al. (1997) highlight, it is more defensible to recognise the uncertainty in model selection and the precision of the parameter estimates than to specify a single-best approximating model which introduces model misspecification bias. We attribute this uncertainty to the high spatial variability in the distribution of koalas. This variability is partly explained by the limited independent effect of the habitat and landscape variables relative to the effect of the spatial autocorrelation term, indicating koalas exhibit spatial behaviour as part of a social or community structure not captured in physical landscape characteristics. Other factors explaining this variability include unmeasured fine-scale habitat heterogeneity, historical disturbance factors such as hunting and wildfire, and the ability of some individuals to survive for a long period in highly fragmented landscapes. The effect of historical hunting is potentially important, with southern Queensland koala populations experiencing high mortality due to harvesting for the fur trade during the late 19th and early 20th centuries, and have not recovered their former abundant status (Gordon and Hrdina, 2005).

4.2. Inferences for koalas

At the site-level, the results of the variable ranking confirm the importance of the proportion of primary tree species.

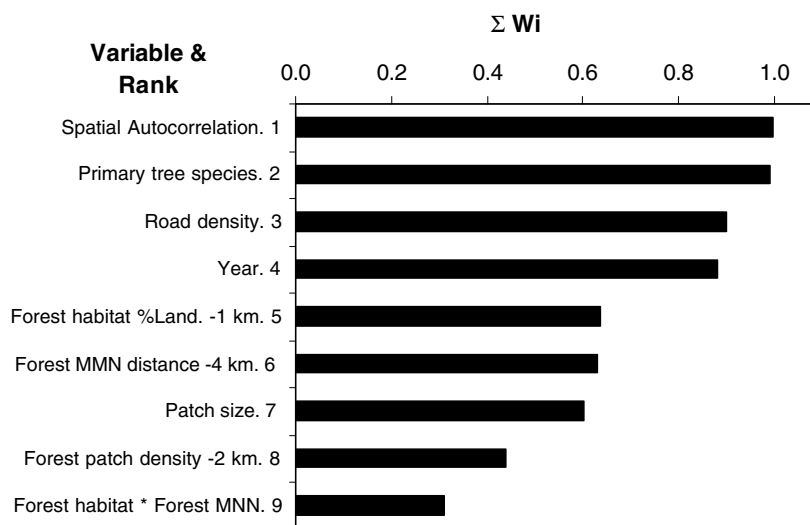


Fig. 5 – Ranking of the variables according to the sum of the Akaike weights ($\sum w_i$) for each explanatory variable, including the spatial autocorrelation term and the year of survey.

Koalas are highly specialised folivores that prefer certain eucalypt species, and the results of our study are consistent with previous studies that koalas preferentially select *Eucalyptus* species with high nutritional value (Cork and Braithwaite, 1996; Cork et al., 1990; Moore et al., 2004b). The importance of preferred *Eucalyptus* species is attributed to koalas' evolutionary habitat requirements which determine its distribution and abundance in the absence of widespread human-induced habitat loss and fragmentation. Tree species' preferences presumably accounted for most of the distribution of koalas within Noosa Shire prior to European settlement in 1860, which subsequently cleared over 50% of favoured eucalypt forests.

At the patch and landscape-levels, the proportion of the landscape occupied by forest habitats had an important influence. However, habitat patch size, the spatial configuration of remaining forest habitats, combined with road density, had a large, combined independent effect that cannot be bypassed in our efforts to conserve this species. Clearing has resulted in the loss of high quality habitat in particular, and thus impacts upon the nutritional resources and reproductive capacity, and hence the distribution and long-term persistence of koala populations. While highly suitable habitats (i.e. habitats dominated or co-dominated by the preferred tree species) should be a priority for koala conservation, we found that all forest habitats, including suitable and marginal habitat categories, were more important than might otherwise be expected. This reflects a more extensive distribution of suitable habitat compared to highly suitable habitat, with suitable habitat having the capacity to support some breeding and low-density koala populations. Connected areas of highly suitable, suitable and marginal habitats are likely to facilitate koala movement and dispersal with a relatively low risk of mortality.

The main cause of the negative effects of landscape configuration is a combination of increased habitat isolation and increased hostility of the matrix with high density of roads. Our observations concur with Fahrig's (2003) interpretation of the negative effects of fragmentation, namely that the overall time spent in the matrix is greater in more fragmented landscapes, which tend to increase the mortality rate and reduce the reproductive rate. While koalas are able to cross non-forest gaps, as forests are cleared and replaced by suburbs and low density rural subdivisions, surviving animals are forced to move across a hostile matrix of cleared land, residential allotments and roads, where the probability of mortality from road deaths and dog attacks is higher.

We found that habitat isolation became increasingly important as the area of forest habitat declined. This interaction effect allows the suggestion to be made that the independent effect of habitat isolation does in fact depend on the area of forest habitat in the landscape. The greater the distance between neighbouring patches, the higher the probability of mortality from dog attacks and vehicle collisions. Roads considerably increase the effect of the land use matrix above the combined independent effects of habitat configuration (Forman et al., 2003). Elevated mortality associated with roads and dog attacks is a serious concern, reducing population growth rates (Dique et al., 2003). In rural landscapes where the land use matrix is less intensively settled, the effect of

configuration is expected to be lower. However, the increased isolation between habitat patches is likely to have significant negative impacts on the energy budget of koalas, with a greater energy budget required in order to access remaining nutritional resources.

A second, and related, reason for negative effects of landscape configuration is the increased abundance of forest fragments. We can infer from the positive effect of habitat patch size, and the negative effect of forest patch density and the mean nearest neighbour distance in the best approximating model, that landscapes composed of small forest fragments have a lower probability of koala occurrence, compared to landscapes with a high proportion of large habitat patches. The independent effects of forest patch density and habitat patch size are secondary to the area of forest habitat and its spatial isolation, but they nevertheless have important negative consequences for koalas. Small, isolated populations of animals have been shown to have a low probability of long-term persistence (Lacy and Lindenmayer, 1995; Lindenmayer and Lacy, 2002). In urban and semi-urban landscapes, human activities in and adjacent to these fragments lead to increased mortality (e.g., dog attacks), which have direct impacts on fitness (Rhodes et al., 2005). If the area of habitat is held constant, the probability of occurrence and long-term persistence of koalas in landscapes with numerous small patches is lower compared to populations occurring in landscapes containing a higher proportion of contiguous habitat patches.

4.3. Inferences for forest-dependent mammals

We can draw several inferences from this koala study for forest-dependent mammals and their sensitivity to the area and the spatial configuration of forest habitat. First, the loss of forest habitat is important for forest mammals, directly impacting on the probability of occurrence, leading to a higher risk of local extinction. Loss of high-quality breeding habitat will trigger a contraction in a species' distribution and, ultimately, its persistence in the landscape. However, the results of this study also indicate that the loss of low-quality habitat also has a negative effect on species occurrence. This result is consistent with Wiegand et al. (2005) who suggested that lower-quality dispersal habitat matters most for those species with intermediate dispersal abilities (such as the koala) living in landscapes composed of small patches of high-quality breeding habitat where surrounding lower-quality habitat enhances the exchange of individuals between patches.

Second, our results differed from Fahrig's (2003) statement that details of how forest habitats are arranged are unlikely to mitigate the risks of habitat loss. Rather, we found that configuration does matter, as does the heterogeneity and hostility of the matrix. Urban and semi-urban landscapes, with a high density of roads, present an extreme case of the negative effects of the land use matrix on movement of individuals. The importance of landscape configuration is variable, and depends on the land use matrix and the ability of species to cross non-forest gaps. These factors may be important for many forest-dependent mammals in fragmented landscapes. For example, Bakker and Van Vuren (2004) found that the fragmentation pattern controlled gap-crossing behaviour in the

red squirrel (*Tamiasciurus hudsonicus*). **Goldingay and Sharpe** (2004) examined the likelihood of survival of populations of squirrel gliders (*Petaurus norfolcensis*) in a set of forest fragments in an urban matrix. They concluded that the greatest challenge is to establish functional corridors. **Lindenmayer and Cunningham** (1997) found that some arboreal marsupials, such as the common ringtail possum (*Pseudocheirus peregrinus*) can tolerate or exploit a *Pinus radiata* matrix, retaining a wide distribution and stable or increasing population, while the greater glider (*Petauroides volans*), that was absent from the matrix, has a more restricted distribution and was more likely to be affected by landscape configuration. In continuous eucalypt forest landscapes, where low habitat quality regrowth forests formed the matrix, **McAlpine and Eyre** (2002) found that landscape configuration was not important for the Yellow-bellied Glider (*Petaurus australis*). These differences relate directly to the intensity of human settlement in the non-forest matrix and the variable ability of forest mammals to utilise and disperse through the matrix. We agree with **Lindenmayer and Lacy** (1995) that forest-dependent mammals are vulnerable to impacts of forest fragmentation, particularly if fragmentation results in very small isolated populations of animals with limited opportunity for dispersal.

4.4. Implications for koala conservation

The koala is listed as vulnerable in New South Wales and in southeast Queensland, and is subject to conservation or recovery plans in both states. Critical to success is the conservation of remaining eucalypt forests, together with spatially targeted restoration programs using local indigenous tree species which increase the size of larger patches and enhance the movement of koalas between neighbouring patches. The decline of the koala over its broad geographic range is primarily a legacy of the extensive clearing of eucalypt forests occurring on fertile soils for agricultural land use over the past 150–200 years (**McAlpine et al.**, 2002). Clearing of native vegetation is now subject to legislation in both Queensland and New South Wales. Urbanisation of the eastern seaboard poses a major contemporary threat to koalas, where clearing is still permitted for urban development. While biodiversity conservation is now a recognised goal in land use planning, it generally remains subordinate to development imperatives in rapidly urbanising regions of southeast Queensland and northern New South Wales. The results of this study highlight the consequences for koala populations of development pressures that continue to clear and fragment eucalypt forests. Furthermore, the intensity of the land use matrix, as indicated by the density of sealed roads, has an important negative effect on koalas. A new planning imperative is urgently required in these regions, which puts biodiversity conservation foremost in the planning agenda.

The results highlight that habitat protection and restoration alone are not sufficient to conserve and restore viable koala populations. Planning should also aim to minimise new urban developments and roads within landscapes occupied by koalas or where koalas are known to have occurred in the recent past. Further, the negative impacts of existing development should be ‘minimised’ by: (i) control of domestic

dogs in areas where koalas occur and also in areas adjacent to koala habitat, especially at night when koalas are most active; (ii) reducing traffic speeds on minor roads, again especially at night; and (iii) the implementation of measures to minimise the risk of vehicle collisions on major roads, whilst also facilitating effective koala movement. To this end, the authors are currently developing spatially explicit planning guidelines for the conservation and restoration of koala populations in fragmented forest landscapes.

A related conservation planning issue emerging from our study is the problem of ecological scale. Scale is of pivotal importance to biodiversity conservation, particularly so, given its relevance to land use decision-making and responsibility for natural resource management and conservation. We have shown that a spatial hierarchy of factors is important for koala conservation in fragmented forest landscapes. The failure to comprehensively understand the importance of working simultaneously at more than one ecological scale has been a limiting factor in koala research and conservation. A key example of this involves a predominant planning focus at the local government level on development assessment at the local scale (1–10 s ha), with broader cumulative impacts on koalas and other wildlife rarely given thorough consideration during the development assessment process. Similarly, regional environmental plans, biodiversity strategies and shire-based strategic planning often lack detailed and reliable strategic integration of biodiversity conservation and land use planning.

5. Conclusion

This study advances our understanding of the relative importance of the area of forest habitat and its spatial configuration on the local occurrence and persistence of fauna populations. First, the research confirms that site-level habitat quality and the area of forest habitat at the landscape-level are key factors impacting on the occurrence of forest-dependent mammals, such as the koala. Conservation efforts should strive to minimise further loss of koala habitat, with emphasis on the highly suitable and suitable habitat classes but also including marginal habitat, which provides important connectivity and dispersal functions. Second, we found that landscape configuration has an important negative effect directly related to the intensity of the land use matrix and increased habitat isolation. We conclude that the area of forest habitat and its spatial configuration, the intensity of the land use matrix, and fine-scale habitat quality are important determinants of koala occurrence, and that landscape configuration cannot be overlooked in the conservation of this species, nor other forest-dependent mammals.

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