

Testing alternative models for the conservation of koalas in fragmented rural–urban landscapes

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Abstract Predicting the various responses of different species to changes in landscape structure is a formidable challenge to landscape ecology. Based on expert knowledge and landscape ecological theory, we develop five competing *a priori* models for predicting the presence/absence of the Koala (*Phascolarctos cinereus*) in Noosa Shire, south-east Queensland (Australia). *A priori* predictions were nested within three levels of ecological organization: *in situ* (site level) habitat (<1 ha), patch level (100 ha) and landscape level (100–1000 ha). To test the models, Koala surveys and habitat surveys ($n = 245$) were conducted across the habitat mosaic. After taking into account tree species preferences, the patch and landscape context, and the neighbourhood effect of adjacent present sites, we applied logistic regression and hierarchical partitioning analyses to rank the alternative models and the explanatory variables. The strongest support was for a multilevel model, with Koala presence best predicted by the proportion of the landscape occupied by high quality habitat, the neighbourhood effect, the mean nearest neighbour distance between forest patches, the density of forest patches and the density of sealed roads. When tested against independent data ($n = 105$) using a receiver operator characteristic curve, the multilevel model performed moderately well. The study is consistent with recent assertions that habitat loss is the major driver of population decline, however, landscape configuration and roads have an important effect that needs to be incorporated into Koala conservation strategies.

Key words: habitat configuration, habitat loss, koala, logistic regression, prediction, road.

INTRODUCTION

Landscape ecology provides an important foundation for the conservation of biodiversity and the management of natural resources (Bissonette 1997; Gutzwiller 2002; Liu & Taylor 2002), and now permeates the fields of forestry, wildlife management, conservation biology, restoration ecology, and urban and regional planning. However, from a wildlife conservation perspective, predicting the various responses of different species to changes in landscape structure is a formidable challenge (Hanski & Ovaskainen 2000; Wu & Hobbs 2002). At the same time, managers are grappling with the problem of how to conserve and restore a range of species living in human-modified landscapes. Reliably identifying those species most vulnerable to landscape change would enable a proac-

tive approach to be taken to conserving and restoring habitats at both the landscape and regional levels (MacNally & Bennett 1997).

One way to make wildlife-landscape studies more proactive and less idiosyncratic is to design tests of current theory before data are collected rather than being derived retrospectively following exploratory data analysis (MacNally & Bennett 1997). A key theoretical issue in these studies is determining the relative importance of landscape composition *versus* landscape configuration (Fahrig 1997, 2003; Villard *et al.* 1999). For many species, landscape composition (Dunning *et al.* 1992) represented by area of suitable habitat type is more influential than spatial configuration (Fahrig 1997, 2003; Trzcinski *et al.* 1999; Villard *et al.* 1999; Lee *et al.* 2002; McAlpine & Eyre 2002). However, recent evidence suggests that landscape configuration becomes important at low levels of suitable habitat, with different species disappearing at different thresholds on the habitat-loss gradient (Andrén 1994;

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With & Crist 1995; Fahrig 2001, 2002). A decrease in the amount of habitat and a corresponding increase in the subdivision of habitat (hereafter referred to as fragmentation) results in a reduction in overall patch colonization rate, while the increase in the amount of edge and reduced habitat connectivity increases the probability of individuals leaving their habitat and entering the hostile matrix, where the death rate is higher (Fahrig 2002). Landscapes also have a temporal as well as spatial component (Marcucci 2000). Exactly how much habitat is enough varies according to a species' life history attributes and the landscape matrix, with species' disappearance from the landscape involving time lags in the order of 10–100 years (Saunders *et al.* 1991; Tilman *et al.* 1994; Hanski 1998; Possingham & Field 2001).

The Koala (*Phascolarctos cinereus*) provides an ideal case study for applying and testing current landscape ecological theory. It is widely distributed, is a multi-habitat species that moves across the landscape, is sensitive to habitat loss and spatial configuration and, where present, it is a flagship species that influences planning, conservation and management (ANZECC 1998; Melzer *et al.* 2000). The Koala is now an Australian faunal icon, although its history since European settlement includes a sustained period of hunting for the fur trade, the records of which help make population changes easier to track. In Queensland, koalas were once abundant, with regulated commercial harvesting operating intermittently from 1906 to 1927 with the annual harvest off-take ranging from about 450 000 to nearly one million (Hrdina & Gordon 2004).

Eighty years later, over most of the geographical range of the Koala across eastern Australia, especially in the states of Queensland and New South Wales, there are local population declines and extinctions. The underlying cause is the continuing growth of the human population along the forested eastern coastal fringe and agricultural expansion in inland regions (Reed & Lunney 1990; Reed *et al.* 1990; ANZECC 1998; Melzer *et al.* 2000). An added conflict with human land use relates to preferential selection by the Koala of certain *Eucalyptus* species, particularly where they occur on higher nutrient soils (Braithwaite 2004; Moore *et al.* 2004; Moore & Foley 2005). This often coincides with areas selected originally for farming which now are the focus of urban growth and coastal development. Although the general pattern of loss of Koala populations has been described, no quantitative studies of the effect of landscape change have been conducted for this species.

This paper aims to explain and predict the occurrence of koalas in a fragmented rural–urban landscape of coastal south-east Queensland (Australia). It addresses the question: can Koala occurrence be reliably predicted from expert knowledge of Koala ecol-

ogy and landscape ecological theory? The study site selected was Noosa Shire for which a detailed ecological history of the Koala has been undertaken, with a particular emphasis on the extent and time of clearing (Seabrook *et al.* 2003). This ecological history provided the historical context for developing a set of nested *a priori* predictions of the multilevel influence of habitat and landscape variables on Koala populations. We empirically tested these predictions using Koala presence/absence data obtained from the now well-tried field method of searching for the presence of Koala faecal pellets (Lunney *et al.* 2000). The predictive models were ranked using several measures of goodness of fit, with the relative importance of key explanatory variables ranked using hierarchical partitioning analysis. The most parsimonious model was evaluated against independent data by calculating the area under the Receiver Operator Characteristic (ROC) curve (Metz 1978). The final model was then compared with the *a priori* predictions to determine their performance and their suitability for further application in two other case studies: Ballarat in central Victoria and Port Stephens in coastal New South Wales.

A priori models

We postulate the following *a priori* models, derived from accumulated knowledge of Koala ecology and landscape ecology theory, of the influence of landscape and habitat variables at three spatial levels: the site or *in situ* level (<1 ha), the patch (1–100 ha), and the landscape (100–1000 ha) (Fig. 1). The models serve as a theoretical construct for integrating knowledge of multiple influences occurring across multiple levels, and provide a basis for the intelligent prior selection of explanatory variables that may influence Koala occurrence (*sensu* Flack & Chang 1987; MacNally 2000). They differ from the traditional null hypothesis testing of single and separable causation. Rather, they provide an integrative approach whereby multiple and only partially separable causes are tested using competing alternative predictions extending over various spatial levels (*sensu* Holling 1998; Burnham & Anderson 2002). Each model also represents a different management alternative for Koala conservation.

Model 1: The quadrat is not dead

This model predicts that the overall proportion of preferred *Eucalyptus* species at sites occurring on high nutrient soils is the major determinant of Koala occurrence, rather than patch or landscape level attributes. The role of nutrition for marsupial folivores is an active field of research, emphasizing the importance of

both nutrients and the role of plant secondary metabolites in plant defence (Moore *et al.* 2004). The findings point to both the relative importance of particular tree species, as well as individual trees at the site level. As eucalypts provide the Koala's main food source, their presence is fundamental to the distribution of koalas across the landscape.

Model 2: The patch matters

This model predicts that the occurrence of koalas at the patch level increases with patch habitat quality, size, increasing shape complexity, and proximity to neighbouring patches of similar quality. High quality habitat is defined from a Koala's perspective as patches with a high proportion of preferred food tree species. Some variation in habitat quality may occur within mapped patches owing to fine-scale heterogeneity in floristic and structural features, soil types, moisture availability and disturbance regimes. Large, high quality habitat patches in close proximity (rather than small, isolated patches) are predicted to have a higher probability of Koala occurrence owing to increased availability of habitat resources, increased connectivity and reduced external pressures from human land use (Hanski 1994, 1998; Hanski & Gilpin 1997).

Model 3: Habitat loss is the major driver

This model predicts that Koala occurrence can be positively predicted by the area of high quality habitat, and that loss of this habitat is the dominant driver of Koala population decline (*sensu* Fahrig 1997, 2003). Drawing on recent empirical evidence of a 40% critical threshold for populations of the yellow-bellied glider (*Petaurus australis*), a large, gliding marsupial, living in continuous eucalypt forests of south-east Queensland (Eyre 2002; McAlpine & Eyre 2002), we predict the presence of a similar habitat retention threshold for the Koala. In comparison to the yellow-bellied glider, which maintains a home range of approximately 40–50 ha, Koala home range size estimates vary from 1 to over 100 ha (Melzer & Houston 2001). A detailed radio-tracking study in an agricultural landscape in south-east Queensland by White (1999) found average home ranges were 34 ha and 15 ha for males and females, respectively, using the 95% kernel, but they were one-third that size using the 70% kernel. Koalas also often move from tree to tree where canopies overlap but, unlike gliders, koalas commonly move across the ground, including open areas between individual trees or patches of trees (Melzer & Houston 2001). Based on knowledge of the home range sizes of these two south-east Queensland arboreal marsupial species, we predicted that an eco-

logical neighbourhood (*sensu* Addicott *et al.* 1987) of ≤ 2000 m was the appropriate spatial extent of landscape analysis for the Koala in the Noosa study. We also expect that time since clearing would further compound the effects of habitat loss. This point had been noted in an historical study of the decline of Koala populations in Port Stephens Shire (Knott *et al.* 1998), with Koala losses taking up to a century as clearing and farming proceeded during the 1800s and remaining Koala populations persisting in areas where clearing did not commence until the second half of the 20th century.

Model 4: Landscape configuration is the strongest predictor

This model predicts that the spatial configuration of individual habitat classes and of all forested habitats combined is the strongest predictor of Koala occurrence, with the probability of Koala occurrence declining with habitat fragmentation and the associated loss of habitat connectivity. In urban and peri-urban landscapes, roads are a dominant landscape element, subdividing habitat, acting as barriers to animal movement and increasing the risk of mortality (Forman *et al.* 2003). Road deaths are recognized as a major source of Koala mortality in fragmented urban landscapes (ANZECC 1998; Lunney *et al.* 2002a; Dique *et al.* 2003). Vehicle mortality continues where roads subdivide Koala habitat, while roads also expose koalas to greater risks of attack from dogs. Dogs gain a predatory advantage when the Koala is forced to travel across open ground, such as when crossing a road (Pieters & Woodall 1996; Lunney *et al.* in press).

Model 5: Global model – combination of all models are important

The global, all inclusive, model combines Models 1–4 to test the prediction that a combination of factors at the three spatial levels is the most reliable predictor of Koala occurrence. It reflects all potential influences depicted in Figure 1, and asserts that Koala occurrence is best predicted and explained by a combination of influences occurring at the site, patch and landscape levels.

METHODS

Study area

Noosa Shire (26.50 S, 152.50 E; 86 823 ha) is located in coastal south-east Queensland, Australia (Fig. 2). It has a subtropical climate, and is biogeographically diverse, ranging from coastal ecosystems occupying

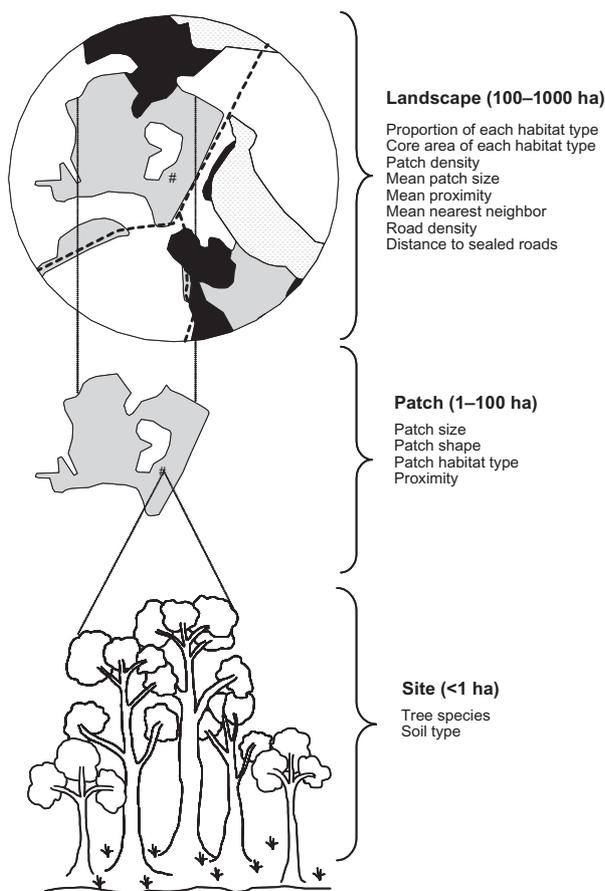


Fig. 1. Multi-level conceptual model of factors influencing Koala occurrence in a fragmented rural-urban landscape of eastern Australia.

Pleistocene sand deposits to subtropical rainforests and wet eucalypt forests on granite intrusions and volcanic soils, and dry eucalypt forests on alluvium and sandstones (Thompson 1992). Landscapes are a mixture of urban and rural land use, and 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. After a period of relative landscape stability between 1940 and 1960, a further 35% loss of remaining habitat occurred as a result of rapid coastal urbanization driven by growth of the tourism industry. Much of the remaining habitat occurs in State Forests (timber reserves) and National Parks, with the latter concentrated on infertile sandy soils in the north of the study area.

Habitat quality classes

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

Table 1. Habitat classes derived for this study by combining the Australian Koala Foundation's Habitat Atlas classification. Australian Koala Foundation (<http://www.savethekoala.com/maps.html>)

Habitat class	Food tree rank % of overstorey
Primary	Primary alone $\geq 30\%$; or Primary and Secondary $\geq 50\%$; or Secondary alone $\geq 50\%$
Secondary	Primary alone $< 30\%$; or Primary and Secondary $< 50\%$; or Secondary alone $< 50\%$
Other	No Primary or Secondary tree species present
Cleared	Agricultural or urban areas largely cleared of native vegetation

Australian Koala Foundation (Callaghan *et al.* 2000) into four habitat quality classes (Table 1). The Koala Habitat Atlas was based on vegetation communities interpreted from aerial photographs (Queensland Herbarium 1998). The habitat quality class for each vegetation community was assigned using the proportional abundance of the identified preferred food tree species (i.e. primary and secondary food tree species) (Callaghan *et al.* unpubl. data 2003). A primary Koala food tree is a *Eucalyptus* species with a significantly higher proportion of surveyed trees having one or more Koala faecal pellets (an indicator of use) compared with other tree species. Similarly, a secondary food tree is a different species of *Eucalyptus* that registers a significantly higher proportion of trees with faecal pellets compared with that observed for remaining species (excluding the primary category). A third category, supplementary food tree species, record a significantly lower proportion of faecal pellets than for secondary species, but greater than for other tree species that generally lack evidence of use by koalas (Phillips & Callaghan 2000; Phillips *et al.* 2000). It is also acknowledged that non-eucalypt species can provide supplementary food resources but, more importantly, eucalypt and non-eucalypt species provide shelter for koalas.

Site selection

Koala survey sites were selected based on a stratification of habitat quality, patch size, distance to sealed roads and a habitat proximity index derived from Hanski (1994) formulation for relative immigration rates. For the proximity index, a maximum threshold distance of 3000 m was set, above which surrounding patches were not considered. This proximity measure was assumed to give a biologically relevant measure of

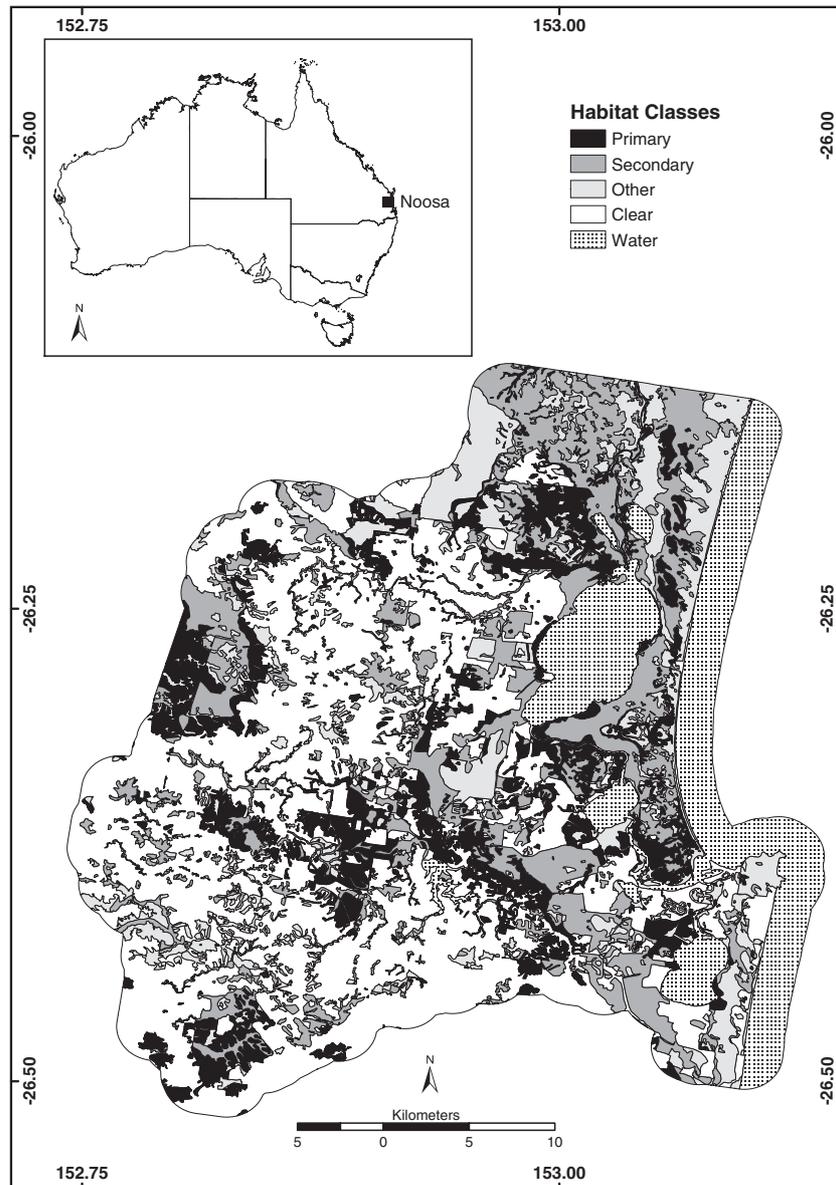


Fig. 2. Location of the Noosa Shire study area.

relative potential immigration from other patches, taking into account differences in habitat quality. Sampling focused on primary and secondary habitats, with larger habitat patches sampled multiple times at varying distance intervals to take into account internal variation in habitat quality and hence resource use by koalas.

Koala faecal pellet surveys

Koalas are often cryptic and are usually difficult to observe in the closed forest habitats that dominate Noosa Shire. For this reason, the presence/absence of

Koala faecal pellets in a quadrat was the preferred survey method. The shape and other characteristics of koala pellets are species-specific, pellets persist after a Koala has departed, and the pellets are reasonably easy to find and can be reliably identified. Disadvantages include the potential for differential pellet decay rates under varying conditions, and the inability to determine the numbers of individual koalas, or their sex, age or reproductive status. The overwhelming advantage is the ability to cover a large area, the size of a shire (10 000–100 000 ha), within several weeks to determine habitat preferences and thus define, rank and map habitats at levels of ecological organization relevant to Koala conservation.

In total, 282 sites were surveyed during the winter and spring of 2001 and 2002. An additional 70 sites previously surveyed (1996–1997), using comparable methods (Australian Koala Foundation unpubl. data 1997), were included to increase sample size ($n = 352$) and spatial coverage. Many of these additional sites were in close proximity to each other and the 2001–2002 sites, thereby increasing the problem of spatial dependence. Each survey site was located in the field using a Global Positioning System. Sites disturbed by recent crown fires were not surveyed. Pellet searches were undertaken at each site according to methods outlined in Phillips and Callaghan (2000) and Phillips *et al.* (2000). A one metre catchment around the base of each tree was searched for up to two-person minutes or until a Koala pellet was found. A presence was recorded for each site where one or more Koala pellets were found. A minimum of 30 trees and a maximum of 36 trees were surveyed at each site.

Spatial autocorrelation

Koalas exhibit spatial behaviour as part of a social structure not captured in physical landscape characteristics; therefore, it was expected that the presence of Koala pellets at a location was dependent upon their co-occurrence in nearby locations. This social structure can be incorporated into a regression model as a spatial autocorrelation term. Each sample point was analysed to determine the neighbourhood effect (White & Engelen 1997) for presence of Koala pellets. This effect was derived by counting the number of presence sites around a sample point within a 0–500 m and 500–1000 m distance interval, weighted to account for area density and the degree of interactions occurring within each distance interval (Fig. 3).

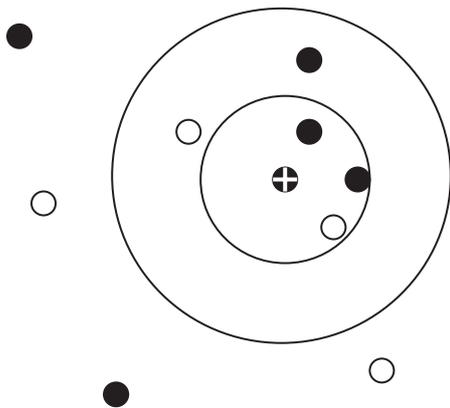


Fig. 3. Neighbourhood effect as indicator for co-occurrence of Koala's presence for sample points. Black dots represent present sites while white dots represent absent sites.

$$N_i = \sum_d \sum_i w_d I_{d,i} \quad (1)$$

Where:

D : neighbourhood effect for sample point I ;
 d : index for distance intervals, i.e. $d = 1$ is 0–500 m, $d = 2$ is 500–1000 m;

w_d : weighting parameter applied to points within interval d ;

$I_{d,i}$: is 1 if sample point I in interval d is 1, otherwise is 0.

Data 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 interval 500–1000 m. This relationship was used to define the weighting parameter for the neighbourhood effect.

Explanatory variables

Site level

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 utilized) categories. Soil classes were derived from classified geology mapping of south-east Queensland at a scale of 1:100 000. Parent geology is a fundamental determinant of the type of soil that develops in any location (Christian & Stewart 1968; McDonald *et al.* 1990). The 81 different lithology units mapped for Noosa Shire were assigned into four broad soil classes: sand, sandy loam, clay loam and clay (Table 2).

Patch level

The focal patch size and habitat class for each survey site were calculated by intersecting the site location with the Koala Habitat Atlas polygons using ArcView GIS Version 3.3 (ESRI 2002). The external boundary of the Habitat Atlas was extended 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). Proximity to neighbouring patches of similar quality was quantified using the habitat mean proximity index described above.

Landscape level

FRAGSTATS Version 3 McGarigal *et al.* (2002) was used to quantify the percent of the landscape (not including water bodies) occupied by primary and secondary habitat (Table 1) at five radial distances

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 = primary, 2 = secondary, 3 = other, 4 = cleared.
Habitat mean proximity index	None	A habitat mean proximity index which measures relative immigration potential from neighbouring patches taking into account habitat quality and patch isolation.
Perimeter:area ratio of focal patch	Ratio	Patch perimeter (m) divided by patch area (m ²) (McGarigal & Ene 2003).
Focal patch size (log value)	Meters	Focal patch size (ha) transformed to log value.
<i>Landscape level</i>		
Proportion of habitat class in the landscape	Percent	The percentage of the landscape occupied by high and medium quality habitat types and the combined percentage of the two habitats.
Time since clearing	Years	Estimated time since clearing based on patterns of land use.
Patch density	Patches/100 ha	Density of total forest patches in the landscape.
Mean nearest neighbour distance	Meters	Euclidean mean nearest neighbour distance (m) between neighbouring forest patches within a maximum search radius of 3000 m (McGarigal & Ene 2003).
Density of sealed roads		Total length of sealed roads (m) divided by the landscape area (ha).
Distance to sealed roads	Meters/hectare	Euclidean distance of site to nearest sealed road.

(1000 m, 2000 m, 3000 m, 4000 m and 5000 m) from each survey site. In addition, the density of primary and secondary habitat patches and their mean patch size were quantified at each extent. To test for the spatial configuration of total forest cover, the four habitat classes were merged into a binary forest/non-forest classification. FRAGSTATS was then used to quantify forest patch density and the mean Euclidean nearest neighbour distance metrics between forest patches at the five radial extents. The density of sealed roads within each of the five radial buffer distances (spatial extent) and the Euclidean distance to sealed roads were calculated using ArcView GIS Version 3.3. Time since clearing was derived from the historical study of Seabrook *et al.* (2003).

Correlation analysis

Correlation analysis was employed to test for collinearity between key explanatory variables at the five spatial extents. Where variables had a Pearson correlation coefficient greater than 0.7, one of the variables was removed (*sensu* Green 1979). To test for spatial variation in the influence of each landscape metric on the dependent variable across the five spatial extents, sin-

gle variable logistic regression (Hosmer & Lemeshow 2000) was applied using R public-domain statistical package (R Project for Statistical Computing release 1.9.0 <http://www.r-project.org>). The Akaike's information criterion or AIC value (Akaike 1973) for each extent was calculated from the model Log-Likelihood. The Akaike weight (Akaike 1983) was then calculated for the five spatial extents. The Akaike weight for a model is the relative likelihood of the model compared with all other models in the set. Finally, we plotted the Akaike weight against the metric mean and standard deviation for each spatial extent, and examined each analysis for similar trends.

Predictive modelling

The predictive modelling had three objectives: (i) select a best approximating model from the *a priori* set of candidate models and verify this model using alternative approaches; (ii) assess the relative importance of the explanatory variables for the final model; and (iii) evaluate the most parsimonious model against an independent data set for the same study area.

First, the data were randomly split 70:30 into a model development set ($n = 245$) and a validation set

($n = 107$). Logistic regression was applied using R-
Version 1.9.0 to develop the predictive models. The
logistic regression model included habitat and land-
scape covariates plus a neighbourhood effect:

$$\ln\left(\frac{P}{1-P}\right) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n D \quad (2)$$

Where:

P is the probability of a Koala pellet presence;

$\beta_0 + \beta_1 x_1 + \dots$ are the linear predictors;

$\beta_n D$ is the last term for neighbourhood effect D .

To select the best approximating model, explanatory
variables were fitted to the logistic regression accord-
ing to the *a priori* models. For Models 1–4, the most
parsimonious model was selected by manual deletion
of variables from the maximal model (Crawley 2002).
Model fit was assessed using the model AIC, the
model residual deviance (Crawley 2002), and the log-
likelihood R^2_L , an analogue coefficient of determina-
tion for logistic regression analysis (Menard 2000).
Key explanatory variables identified in Models 1–4
were used for the selection of Model 5. We tested for
significant plausible interactions between the remain-
ing variables (e.g. patch size and habitat type; propor-
tion of preferred tree species and proportion of
suitable habitat in the landscape). Because of the large
number of key explanatory variables ($n = 12$) and
hence model combinations, we applied the ‘all.regs’
function of the R-package ‘hier.part’ (MacNally &
Walsh 2004) to select the minimal Model 5 from all
model combinations based on the model AIC and R^2_L
values.

To select the best approximating model from the five
a priori models, we ranked Models 1–5 in order of
their level of empirical support using Akaike weights,
with weight values >0.9 indicating a high level of sup-
port for a particular model (Burnham & Anderson
2002). We also tested for significant differences in
model deviance between model pairs using the chi-
square test (Crawley 2002). To test for collinearity
between explanatory variables in the final model, we
assessed the total independent contribution of each
explanatory variable relative to its joint contribution
using hierarchical partitioning analysis (Chevan &
Sutherland 1991; MacNally & Walsh 2004). Highly
collinear variables have a large joint effect in relation
to their independent effects. Finally, a backward step-
wise regression was applied using a subset ($n = 24$) of
explanatory variables as inputs to provide a compar-
ison to the results of the *a priori* model selection
process.

For the second modelling objective, we ranked the
relative importance of explanatory variables in the
final model using hierarchical partitioning analysis.
For the third objective, we first quantified the Pearson
residuals of the best approximating model, and also
for the same model applied to the validation data, and

mapped their distribution to assess spatial patterns of
unexplained variation. Second, we evaluated the final,
most parsimonious model against the independent
validation data set using the area under the ROC curve
(Metz 1978; Pearce & Ferrier 2000). The area under
the curve can be interpreted as the probability that a
randomly chosen, truly occupied site is correctly
ranked relative to a randomly chosen unoccupied site.
The discrimination performance of the model equates
to the proportion of validation sites correctly predicted
to be occupied (sensitivity) and the model specificity,
or proportion of absence sites correctly predicted.
Threshold values were fitted incrementally on a scale
of 0.0–1.0 using the R package ROC (BioConductor
Project release 1.3, <http://www.bioconductor.org>).

RESULTS

Spatial extents

Koala pellets were present in 202 sites and absent from
150 of the total sites surveyed. There was no single
spatial extent at which key landscape metrics had the
strongest effect on the presence/absence of Koala pel-
lets. Similarly, there was no evidence that the spatial
variation in the mean and standard deviation of the
metric values was correlated with the Akaike weight
values of the single-variable logistic regression models
for the five spatial extents (Fig. 4). For the individual
metrics, there was a high level of support for the
proportion of the landscape occupied by primary
habitat ($w_i = 0.965$) and the density of sealed roads
($w_i = 0.995$), both at the 1000-m spatial extent. The
4000-m spatial extent had a high level of support
($w_i = 0.800$) for the mean nearest neighbour distance
between forest patches. In contrast, the proportion of
the landscape occupied by secondary habitat, and the
density of primary and secondary habitat patches
showed relatively low Akaike weight values for all spa-
tial extents. The 1000- and 2000-m spatial extents
showed the strongest effect for the density of forest
patches.

Explanatory variable collinearity

Overall, there was a low to moderate level of colinear-
ity between the final-subset of explanatory variables
(Table 3). Variables showing the highest level of colin-
earity included: patch size and perimeter:area ratio
($r = -0.77$); the habitat mean proximity index with the
spatial autocorrelation term D ($r = 0.60$); the habitat
mean proximity index with the proportion of primary
habitat ($r = 0.40$) and cleared habitat ($r = -0.54$); the
proportion of cleared habitat with the proportion of
primary habitat ($r = -0.48$) and secondary habitat

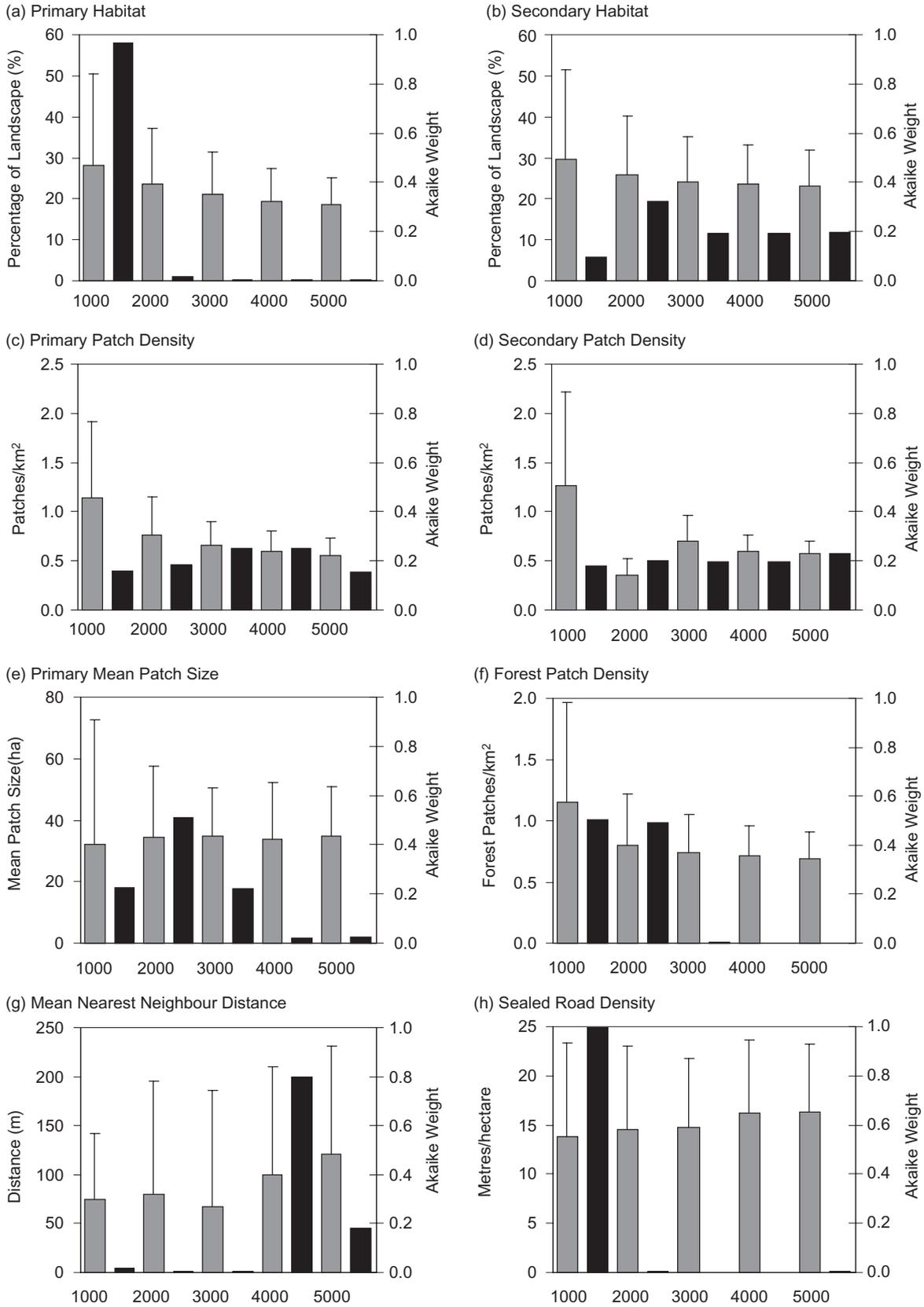


Fig. 4. Mean (grey shading), standard deviation (error bars) and Akaike weights (w_i) (black shading) of key landscape level predictors at increasing spatial extents from Koala survey sites.

Table 3. Correlation matrix of Pearson's correlation coefficients for key explanatory variables

Variable	Var1	Var2	Var3	Var4	Var5	Var6	Var7	Var8	Var9	Var10	Var11	Var12	Var13	Var14
Primary tree species	1													
Patch size	-0.05	1												
Perimeter:area ratio	-0.04	-0.77	1											
Habitat mean proximity index	-0.17	0.38	-0.31	1										
Primary habitat	-0.08	0.20	-0.24	0.40	1									
Secondary habitat	-0.04	0.26	-0.22	0.29	-0.42	1								
Cleared habitat	0.03	-0.41	0.46	-0.54	-0.48	-0.46	1							
Primary mean patch size	0.02	0.16	-0.19	0.24	0.67	-0.35	-0.31	1						
Distance sealed roads	0.18	0.03	-0.08	0.10	0.08	0.02	-0.21	0.02	1					
Road density	-0.14	-0.21	0.27	-0.18	-0.20	-0.14	0.41	-0.07	-0.48	1				
Proximity index	-0.14	0.22	-0.16	0.48	0.05	0.46	-0.40	-0.04	0.30	-0.10	1			
Forest patch density (2 km)	0.04	-0.23	0.27	-0.35	-0.20	-0.34	0.61	-0.02	-0.34	0.40	-0.45	1		
Mean nearest neighbour (4 km)	0.10	-0.03	0.03	-0.50	-0.20	-0.19	0.33	-0.09	-0.07	-0.05	-0.40	0.13	1	
D	0.05	0.18	-0.19	0.60	0.29	0.06	-0.34	0.25	0.19	-0.17	0.04	-0.18	-0.30	1

Correlated variables with $r \geq \pm 0.40$ are bold.

($r = -0.46$), and also with forest patch density ($r = 0.61$).

Predictive models

Model 1 predicted that the probability of a Koala pellet being present increased with the occurrence of primary tree species and soil fertility. The spatial autocorrelation term D made a strong contribution to the performance of Model 1, as it did for Models 2–5. The interaction between the soil fertility classes and the proportion of preferred tree species did not improve the overall model fit and was not included. The fit of Model 1 was poor, with a high residual deviance compared with the degrees of freedom, indicating model over dispersion (Table 4).

Model 2 predicted that the probability of the presence of a Koala pellet increased with the log of patch size and habitat quality, and decreased with the habitat mean proximity index. The perimeter:area ratio was not included in the final model because of its strong correlation with patch size (Table 3). The effect of patch size was stronger than habitat quality, with the interaction between patch size and habitat quality not contributing to an improvement in model fit. Koala pellet presence is concentrated in large, irregular shaped patches > 100 ha. Below this patch size threshold, an increased proportion of absent sites was observed. Model 2 deviance and measures of fit were a significant improvement on Model 1, although Model 2 was over dispersed.

Model 3 predicted that the probability of a Koala pellet being present increased with the proportion of the landscape occupied by primary and secondary habitats combined at the 1000-m spatial extent. The proportion of both habitat types combined made a stronger contribution to the model fit than did the proportion of primary habitats alone, indicating that both habitat types are important for koalas. This result is consistent with our prediction for Model 3. No clear habitat retention threshold was observed at the 1000-m extent, with a steady decline observed in the probability of pellets being present as the proportion of primary and secondary habitats declined. At the 45–50% habitat proportion, there was a 50% chance of Koala pellet presence, while at the 20% proportion there was a 20% chance of a pellet being present at a site (Fig. 5). As predicted, rural landscapes cleared for over 100 years had a lower probability of koalas being present. This temporal effect was closely linked with the spatial effect of intact, forested landscapes compared with fragmented urban and rural landscapes. Model 3 deviance was not a significant improvement on Model 2, although the measures of fit and model deviance did indicate a slight improvement (Table 4).

Table 4. Rank of the final five predictive models using Akaike weights (w_i) derived from model AIC, model residual deviance, and the log-likelihood coefficient of determination R^2_L

Rank	Model	K	AIC	w_i	Residual deviance	d.f.	R^2_L	P -chi-square
1	Model 5	7	285.7	0.999	275.2	238	0.250	NA
2	Model 4	4	300.0	0.001	290.6	241	0.198	0.002 (M4–M5)
3	Model 3	3	309.5	0.000	303.4	243	0.166	0.001 (M3–M4)
4	Model 2	4	311.1	0.000	303.1	240	0.133	0.965 (M2–M3)
5	Model 1	3	315.9	0.000	309.9	241	0.093	0.030 (M1–M2)

The significance of difference in model deviance between the model pairs is measured by the probability of chi-square. K, number of model parameters, excluding the model intercept; M (as in M1–M5), Model; NA, not applicable.

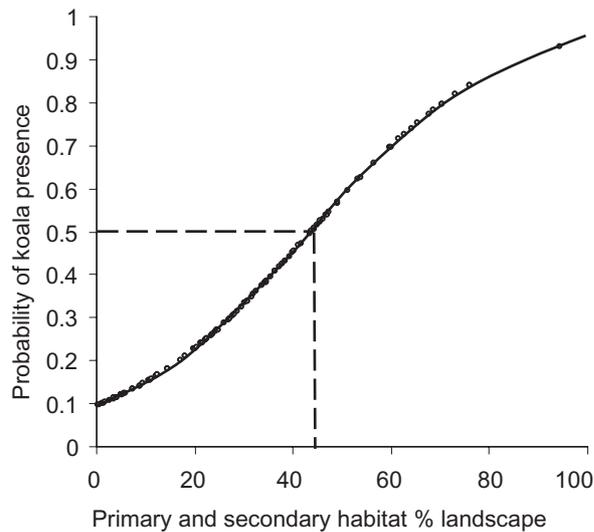


Fig. 5. Relationship between proportion of primary and secondary habitat remaining and predicted probability of Koala occurrence. Curve is derived from univariate logistic regression model.

Model 4 predicted that the probability of a Koala presence increased with the mean patch size of primary habitats, but declined with the density of sealed roads at the 1000-m extent, density of forest patches at the 2000-m extent, and mean Euclidean nearest neighbour distance between forest patches at the 4000-m extent. The negative effect of the density of sealed roads is consistent with our prediction that roads are detrimental to the survival of Koala populations in rural–urban landscapes. The negative relationship with the density of forest patches and mean nearest neighbour distance also is consistent with the prediction that increased fragmentation and isolation of forest patches negatively impact on Koala occurrence. Model 4 deviance was a significant improvement on Model 3 (P -chi-square = 0.001), although the model remained over dispersed (Table 4).

Model 5, the global model, included variables for each level of influence, with positive effects for the

proportion of preferred tree species, the log of focal patch size, and the combined proportion of the landscape occupied by primary and secondary habitats. Negative effects were attributed to the habitat mean proximity index, density of sealed roads, the mean nearest neighbour distance between forest patches at the 4000-m spatial extent, and the density forest patches at the 2000-m extent. The density of forest patches had a moderate joint effect with proportion of primary and secondary habitat, but was retained because it made a positive contribution to the model fit. Soil, habitat quality, time since clearing and mean patch size of primary habitats were excluded from the final model as they resulted in a less parsimonious model. There was a moderate interaction effect between the proportion of the primary tree species at the site level and the proportion of primary and secondary habitat although this did not improve model fit. Model 5 deviance was a significant improvement on Model 4 (P -chi-square = 0.001), as was model fit (Table 4).

The results of the backward stepwise regression produced a less parsimonious model ($K = 11$; AIC = 292.3; $R^2_L = 0.247$), but a similar residual deviance (272.29 on 236 d.f.). Eight variables were common to Model 5: proportion of primary tree species, log focal patch size, habitat mean proximity index, the proportion of primary and secondary habitat at the 1000-m extent, density of sealed roads at the 1000-m extent, forest mean nearest neighbour distance at the 4000-m extent, forest patch density at the 2000-m extent, and the spatial autocorrelation term. Three new variables were included: distance to sealed roads, proportion of primary habitat, and the proportion of secondary habitat.

Ranking of *a priori* models and explanatory variables

There was a high level of empirical support for Model 5 ($w_i = 0.999$), but negligible support for Models 1–4 ($w_i \sim 0$) (Table 4). A similar ranking was observed for

the residual deviance for the five models, the likelihood ratio coefficient of determination R^2_L , and the comparison of the P -chi-square between paired models (Table 4).

The combined independent effect of the key explanatory variables accounted for 55% of the total explained variation, with a 45% combined joint effect (Fig. 6). The proportion of the landscape occupied by primary and secondary habitat and the spatial autocorrelation term D had the highest independent contribution, followed by mean nearest neighbour distance between forest patches, forest patch density, road density, focal patch size, habitat mean proximity index and the proportion of primary tree species. The addition of the density of forest patches resulted in a 4.6% decrease in the joint contribution of the proportion of the landscape occupied by primary and secondary habitat, further indicating colinearity between these variables.

Model evaluation

The Pearson residual values for Model 5 ranged from -3.44 – 2.0 , and were relatively evenly distributed across the study area (Fig. 7a). Residual values were higher in intact habitats occurring in State Forests and National Parks, indicating that other factors not included in the model probably influence Koala occurrence in these areas. In contrast, the residual values from the evaluation data set showed an even spread of low residual values across the study area, with the exception of a cluster of two sites in the west and one in the centre of Noosa Shire (Fig. 7b). The area under the ROC curve (AUC) was 0.77 ± 0.05 , indicating reasonable overall accuracy of the model. An AUC of

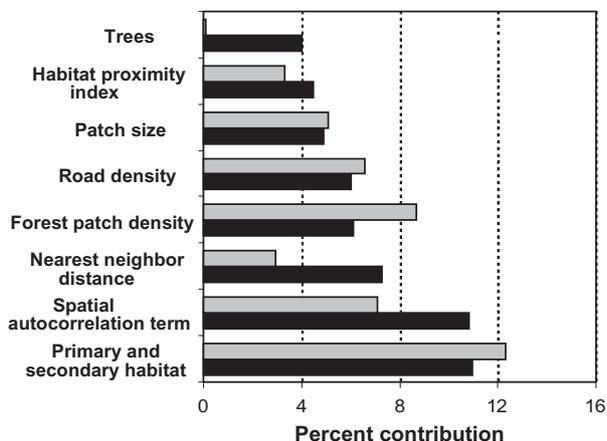


Fig. 6. Rank of the key explanatory variables according to their independent contribution (black shading) to the total explained variation of the most plausible model (Model 5). Joint contribution (grey shading) indicates the percentage contribution shared with other variables in the model.

0.5 is a random distribution while $AUC > 0.9$ shows a strong discrimination, i.e. the ability to predict correctly sites with and without Koala pellets. The proportion of present sites (model sensitivity) correctly predicted was 0.77, while the proportion of negative sites (model specificity) was 0.68.

DISCUSSION

Approach and model performance

In this case study, we chose a nested set of models based on existing literature about koalas and landscape ecological theory to test the relative importance of habitat loss, landscape configuration, plus other habitat and land use variables on Koala presence/absence. *Post hoc* examination of the results of model testing identified that the initial predictions were supported by analysis of the data for Noosa Shire. The ranking of the final models and the explanatory variables for the global model confirm the importance of the landscape level analysis and, critically, the proportion of the landscape occupied by high quality habitat. This result reinforces the assertion by Fahrig (1997, 1999, 2003) that habitat amount is more important than configuration. However, configuration has an important secondary effect on Koala occurrence independent of habitat amount, with this effect attributed to fragmentation and spatial proximity of total forest cover plus the proximity of large, high quality habitat patches. What we were not able to predict well was the spatial extent at which the effect of habitat loss, and especially habitat configuration, were the most important for the Koala. The 1000-m radial extent for habitat is at the lower end of predictions, while the influence of the mean nearest neighbour distance between forest patches at the 4000 m extent was partially unexpected. It arose from insights developed after examining the Akaike weights for each of the five radial extents.

In comparison, the backward stepwise regression, while producing a parsimonious model fit, failed to discriminate between the ecologically similar proportions of primary habitat and secondary habitat, and their combined proportion. A similar problem occurred for the road metrics, density of sealed roads and distance to sealed roads. This outcome is consistent with Flack and Chang (1987) and MacNally (2000) who argued that automated approaches to model selection do not equate to identifying independent variables that are most likely to influence the dependent variable.

The over dispersion and moderate level of discrimination of the final global model is largely due to a small subset of high-residual absence sites ($n = 25$)

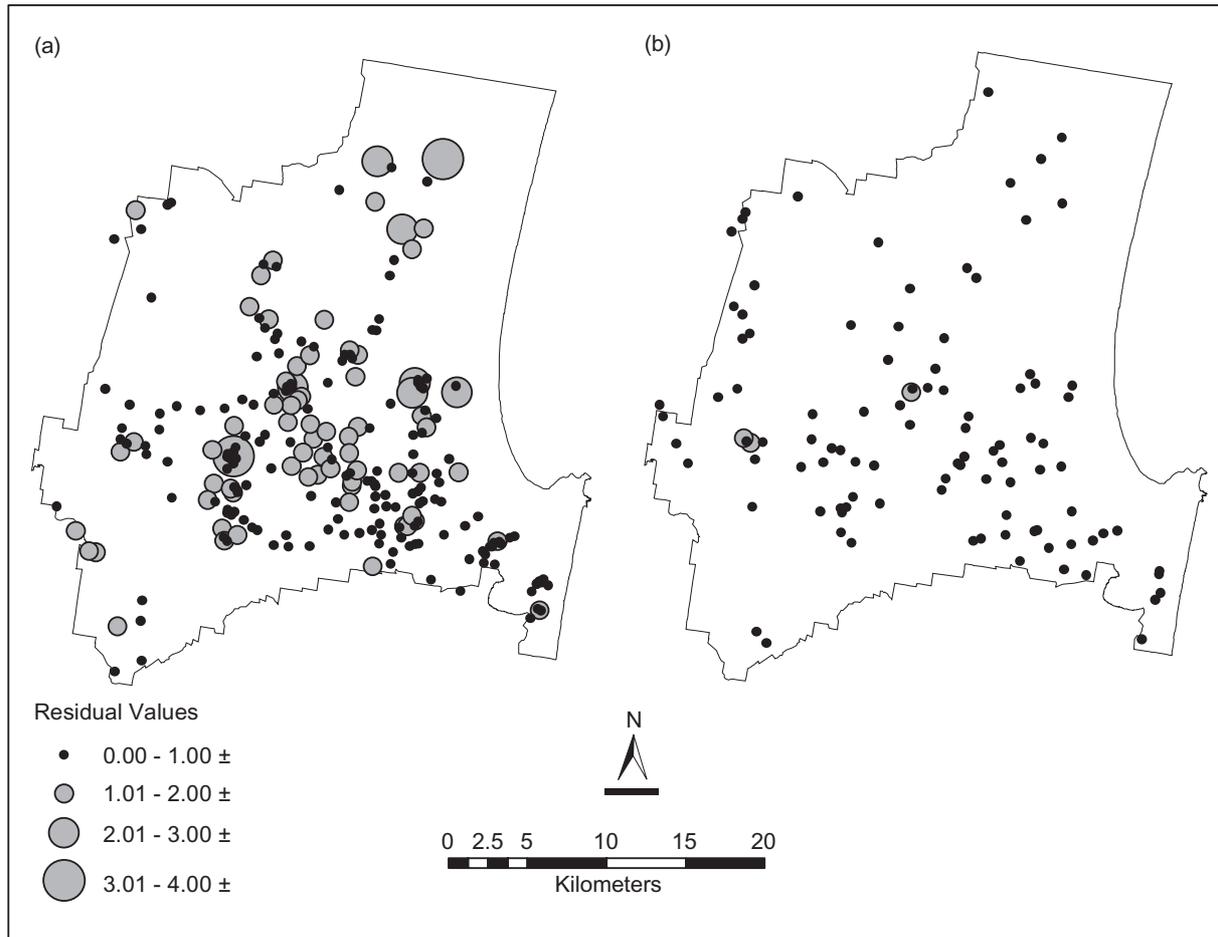


Fig. 7. Spatial distribution of residuals for: (a) the most parsimonious model – Model 5 and (b) for the same model applied to the validation data set.

occurring in intact landscapes located within State Forests and National Parks. These sites have a high proportion of suitable habitat at the landscape level, but a low proportion of primary tree species at the site level. Consequently, the sites are less attractive to koalas. One possible explanation is the fine-scale spatial heterogeneity in tree species composition, soil moisture and fire history within these intact landscapes. This heterogeneity was evident during field work, and partially explains the moderate interaction effect detected between the proportion of the primary tree species and the proportion of primary and secondary habitat. The removal of these sites overcame the problem of over dispersion, and improved model performance ($R^2_L = 0.28$; area under the ROC = 0.80). However, we opted to retain the outliers because their removal unrealistically inflated the predictive performance of the model and over-simplified the factors influencing the occurrence of koalas in Noosa Shire. All the R^2_L values in this study are low compared with the R^2 values typically encountered in good linear regression models. However, as Hosmer

and Lemeshow (2000) highlighted, low values are the norm in logistic regression, and this presents a problem when reporting their values to an audience accustomed to the higher linear regression values.

Pattern and process

Two landscape level processes appear to be important for the Noosa Koala population. First, the historical and ongoing loss of habitat continues to impact negatively on their distribution, with the probability of Koala occurrence steadily declining with the incremental loss of both primary and secondary habitat. Secondary habitat emerges as ecologically more important than originally predicted. This reflects the fact that secondary habitat is the most extensive habitat class, providing medium-quality food resources and facilitating dispersal. Hence, both primary and secondary habitats are vital for the survival of the Noosa Koala population. Koala populations in Noosa Shire, as elsewhere in south-east Queensland, are

declining in rural and urban landscapes that are still relatively intact, signifying that non-habitat factors are contributing to their decline. While we have taken landscape history into account, unexpected absence of koalas from intact habitats may be due to elevated rates of mortality from dog attacks, traffic or wildfires. This is indicative of our inability as yet to measure all possible causal factors, hence the moderate level of discrimination achieved by the final global model.

Second, spatial configuration of total forest cover and to a lesser degree, high quality habitats, is important for Koala movement. As forests are cleared and replaced by suburbs and low density rural subdivisions, koalas are forced increasingly to move across the matrix of cleared land, residential allotments and roads where the probability of mortality from road deaths and dog attacks is considerably higher (Lunney *et al.* 2002b). We considered forest fragmentation and roads as being two aspects of the conversion of forested land into a patchwork of rural farms and urban areas intersected by roads. In most real landscapes, fragmentation does not generally occur without roads and roads cannot be constructed without fragmentation (Forman 1995). Elevated mortality associated with roads is a serious concern, reducing population growth rates and hence viability through vehicle collisions and dog attacks (*sensu* Fahrig *et al.* 1995; Dique *et al.* 2003). Understanding the implications of these processes for population dynamics is crucial for designing effective Koala conservation management strategies.

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