

The importance of integrating landscape ecology in habitat models: isolation-driven occurrence of north island robins in a fragmented landscape

Yvan Richard · Doug P. Armstrong

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Abstract Although the role of habitat fragmentation in species declines is well recognised, the effect of habitat quality on species distributions is often studied using presence–absence models that ignore metapopulation dynamics. We compared three approaches to model the presence–absence of North Island robins in 400 sites among 74 fragments of native forest in a 15,000-ha agricultural landscape in New Zealand. The first approach only considered local habitat characteristics, the second approach only considered metapopulation factors (patch size and isolation), and the third approach combined these two types of factors. The distribution of North Island robins was best predicted by patch isolation, as their probability of occurrence was negatively correlated with isolation from neighbouring patches and from the closest major forests, which probably acted as a source of immigrants. The inclusion of habitat factors gave only a slight increase in predictive power and indicated that robins were more likely to occur in areas with tall canopy, tall understorey and low density of young

trees. We modelled the effect of isolation using an index of functional patch connectivity based on dispersal behaviour of radio-tracked juveniles, and this functional index greatly improved the models in comparison to classical indices relying on Euclidean distances. This study highlights the need to incorporate functional indices of isolation in presence–absence models in fragmented landscapes, as species occurrence can otherwise be a misleading predictor of habitat quality and lead to wrong interpretations and management recommendations.

Keywords *Petroica longipes* · Presence–absence · Metapopulation · Habitat quality · Connectivity · Patch isolation · Dispersal · Species distribution

Introduction

Identifying factors driving the distribution of species is at the core of ecology, and is important for developing strategies to prevent further loss of biodiversity. Habitat fragmentation has been identified as a major cause of species decline worldwide (Saunders et al. 1991; Vitousek et al. 1997). At a local scale, it can lead to habitat deterioration via edge effects, a decrease in food availability, and an increase in predators, parasite abundance or disease prevalence (Saunders et al. 1991; Paton 1994; Andren 1995; Burke and Nol 1998; Harrison and Bruna 1999; Doak 2000; Chalfoun et al. 2002). At a broader

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Y. Richard (✉) · D. P. Armstrong
Wildlife Ecology Group, Institute of Natural Resources,
Massey University, Private Bag 11 222, Palmerston
North, New Zealand
e-mail: y.richard@massey.ac.nz

spatial scale, habitat fragmentation can impede the exchange of individuals between (sub-) populations, leading to a diminished rescue effect or to increased inbreeding (Caughley 1994; Brown and Kodric-Brown 1977; Pulliam 1988; Sih et al. 2000; Reed 2004).

Presence–absence data have been commonly used to identify habitat characteristics correlated with species distribution, and in turn for determining suitable habitats for reintroductions or protection (Van Teeffelen et al. 2006). It is relatively easy to collect data on a range of habitat characteristics as well as presence–absence of species, hence the approach has been used for a wide range of applications (e.g., Lawton and Woodroffe 1991; Rushton et al. 2000; Smart et al. 2000). However, a shortcoming of the approach is that a good quality patch might be unoccupied because of chance events related to metapopulation dynamics, i.e., a small isolated patch may not be recolonised after a local extinction regardless of its quality (Hanski 1998). On the other hand, species can be present in low quality sink habitats due to dispersal from higher quality habitats (Pulliam 1988). Consequently, although presence or absence (or density) of a species is often directly related to habitat quality (Bock and Jones 2004), it may be a misleading indicator in some situations (Van Horne 1983).

Metapopulation dynamics, although likely to mask the true relationships between habitat and species occurrence, are often not considered in presence–absence models, with alternative models only considering different aspects of local habitat quality driving occupancy. In contrast, many other presence–absence models take metapopulation dynamics into account by relating probabilities of colonization and extinction to patch size and isolation (Hanski 1998), but do not consider local habitat quality (but see Moilanen and Hanski 1998). Armstrong (2005) referred to these alternative modelling approaches as following the “habitat paradigm” and “metapopulation paradigm” respectively, and noted that published presence–absence studies fell into four groups: (1) habitat paradigm; (2) metapopulation paradigm; (3) integrating elements of both paradigms; and (4) theoretically ambiguous (the final group consists of studies reporting area effects with no data that can be used to resolve effects of patch area on habitat quality and probability of chance extinction).

Although it seems sensible to integrate the two paradigms by including patch isolation in species–habitat models as well as local habitat factors, isolation can be difficult to define. Patch isolation indices used in the literature are often calculated from the Euclidean distances to the nearest neighbouring patches (e.g., Doebeli and Ruxton 1998; Hanski et al. 2000), sometimes correcting for their area, quality, and occupancy (e.g., Moilanen and Hanski 1998). However, isolation indices based on Euclidean distances assume a random dispersal behaviour and a homogeneous matrix between patches, and are often poor predictors of species movements (Winfree et al. 2005). Patch isolation should be defined relative to species movement behaviour, as the existence of corridors or barriers in the matrix has been shown to greatly enhance or impede individual movements between patches (Potter 1990; Ricketts 2001; Gobeil and Villard 2002; Goodwin and Fahrig 2002; Haynes and Cronin 2006).

Presence–absence data for this study were collected for the North Island robin (*Petroica longipes*) in the central North Island of New Zealand. Robins are an ideal model species for this research as they are locally abundant, although absent in some forest patches (Robertson et al. 2007), sedentary, and easy to detect. This species is also interesting from a conservation point of view as its range has greatly declined since human settlement in New Zealand (Bell 1986).

The purpose of this study is two-fold. Firstly, we compared three possible approaches for analysing presence–absence data in a fragmented landscape. The first approach only includes habitat factors and thus follows the “habitat” paradigm whereas the second approach only considers the size of habitat patches and their isolation from putative source populations and from neighbouring patches, thus following the “metapopulation” paradigm. The third approach combines the two paradigms by incorporating both habitat and metapopulation factors. Although many studies incorporated both types of factors, this study is to our knowledge the first to compare explicitly these different approaches. Secondly, we compared the predictive power of several indices of patch isolation for explaining the distribution of North Island robins. In particular, we were interested in assessing the predictive power of an index of patch connectivity based on the functional

distance between patches that takes into account the connectivity of the matrix between patches, and calibrated from actual data on juvenile robin dispersal (Richard and Armstrong 2010).

Methods

Model species and study area

The North Island robin (*Petroica longipes*) is a small (26–32 g) insectivorous passerine endemic to New Zealand (Heather and Robertson 2000). Its habitat is typically native podocarp-broadleaf forest, but it can also be found in *Pinus radiata* (exotic pine) plantations. The North Island robin is a non-migratory species, is socially monogamous, shows high site fidelity, and feeds mainly on invertebrates in the leaf litter. Robins usually undergo a dispersal phase shortly after fledging, then stay on the same territory for the rest of their lives (Higgins and Peter 2002). They are highly territorial and inquisitive, and respond strongly to territorial calls, giving them a very high detectability. Indeed, a survival study using capture-recapture models on adult robins in a mainland forest fragment using the same methodology to detect individuals estimated a probability of recapture of 0.94 (Armstrong et al. 2006).

The study area of 15,000 ha was located in the central North Island of New Zealand, between the township Benneydale (175°22' E, 38°32' S) and Pureora Forest Park. The landscape is mainly farmland, with some forest remnants varying in shape, quality and isolation of the continuous podocarp-broadleaf forest that previously covered 96% (Ewers et al. 2006) of the North Island before human colonisation 800 years ago (Anderson 1991). The area is bordered to the east and south by exotic plantations of *Pinus radiata*.

Data

Data on robin presence–absence were collected between September and May in 2004–2005 in 400 sampling sites in 74 forest patches. A patch was defined as a minimum area of 0.5 ha of native forest with canopy > 2.5 m, separated by at least 75 m of pasture from other forest habitat, the approximate diameter of a robin territory at high density. Sampling

sites were separated by 150 m to reduce the chance of multiple records of the same individuals (our experience with banded robins suggests that robins are unlikely to be attracted over this distance). At each site, the spatial coordinates were recorded with a handheld GPS, and only one researcher (YR) visually assessed a set of habitat variables within a 50-m radius, ensuring the measurements were consistent among sites. The approximate heights of both the tall canopy (trees > 15 m high) and secondary canopy (trees 2–15 m high) were recorded. The densities of both tall and small trees were recorded, as the average distance between a tree and its nearest neighbour, as well as the mean diameter-at-breast-height (DBH) of the tall trees. The average height of the understory (vegetation < 2 m) was also estimated, as well as the density of vines categorized in four subjective classes (1 in absence of vines to 4 for a dense wall of vines). Finally, the distance to the closest stream was recorded if one was present within a 75 m radius around the location, or was otherwise extracted from the geographical information system (GIS; see below).

Presence or absence of robins was then recorded by playing a lure territorial call for one minute and scanning the habitat for two additional minutes. Trials in the field indicated that this duration was sufficient to detect robins whose territories encompassed the sampled site, but short enough to prevent individuals attracted by the lure tape from moving to habitats where they would not naturally occur.

The locations were then input in a GIS using ArcGIS version 9.0 (ESRI, Redlands, California, USA). The GIS included the vegetation cover map of the study area and additional remote sensing habitat variables obtained from Landcare Research (Palmerston North, New Zealand). The two-dimensional map of the vegetation cover of the study area was digitised at 15-m resolution from recent high-resolution aerial photographs (from 2000) and satellite images (LANDSAT and SPOT5 from 2002) using ERDAS Imagine 8.5 (Leica Geosystems®) in order to accurately represent all the woody vegetation including isolated trees potentially used by dispersing juveniles (Richard 2007). Four vegetation types were recognised and defined as mature native forest, plantation forest of *Pinus radiata*, shrubs, and pasture. We validated this classification in the field by visiting each part of the study area over 3 years, checking for

the agreement between the map and our classification, and we made modifications where necessary. The minimum slope was calculated from a 50-m radius buffer around each recorded site because robins are thought to prefer flat areas to establish their territories (Clubb 2003). The distance to the closest forest edge and the elevation (from the Land Environment of New Zealand database; Leathwick et al. 2003) were also calculated from the GIS, as these factors can potentially affect habitat quality.

In order to incorporate metapopulation dynamics in the models, we calculated the area (ha) of each patch using ArcGIS, and assigned an index of shape and isolation to each patch. The shape was defined as:

$$\text{Shape} = 0.282 \cdot \frac{\text{Perimeter}}{\sqrt{\text{Area}}},$$

following Farina (1998), with values from zero for perfectly circular patches to infinity for increasingly complex shapes. Additionally, we developed a program in Python for ArcGIS to calculate an index of functional patch connectivity (IFPC; program available at <http://www.massey.ac.nz/~yrichard/IFPC>), which is inversely related to patch isolation. This index is the sum of the ratio between the area and the inter-patch cost distance (edge to edge) for all neighbouring patches within 2 km of the focal patch (See Appendix 1 in Electronic Supplementary Material), but does not consider the area of the focal patch. It differs from the traditional proximity index of Gustafson and Parker (1994) in that the latter considers the Euclidean distance between patches whereas IFPC takes into account the likelihood of movement based on the permeability of the matrix between patches (See Appendix 1 in Electronic Supplementary Material). The calculation of IFPC relies on a cost raster map, where each pixel indicates the resistance to movements across it, which was calibrated using actual data on the dispersal of juvenile robins in the same study area (38 juveniles, 220 dispersal steps; Richard and Armstrong 2010). This index considers the dispersal behaviour of the species, and thus represents a more realistic measure of patch isolation than the traditional ones relying on the Euclidean distance to neighbouring patches (e.g., Doebeli and Ruxton 1998; Hanski et al. 2000).

In addition to IFPC, two traditional measures of patch isolation were calculated for each patch using ArcGIS for comparison: the edge-to-edge Euclidean

distance to the nearest patch, and the proximity index of Gustafson and Parker (1994) which is the same as IFPC but using Euclidean distances instead of cost distances.

The forests surrounding the study area contained a relatively high density of robins. Pureora Forest Park, located 10 km to the east, is a natural reserve managed by the Department of Conservation where robins benefit from a relatively high productivity and survival because exotic predators such as rats (*Rattus* spp.), mustelids (*Mustela* spp.) and brush-tailed possums (*Trichosurus vulpecula*) are regularly controlled by poison operations. We therefore suspected that these forests could act as source populations and provide immigrants to the study area. The functional distance to the closest major forest, calculated as the cost distance between each patch and the closest surrounding major forest (cost distance to continuous forest, CDCF) was therefore calculated, using the same cost map as in the calculation of the IFPC, as well as the Euclidean distance for comparison.

In order to normalise the variables we considered, the distance to closest edge, the slope, the patch area, the IFPC, the distance to the nearest neighbouring patch and the proximity index were log transformed, and the distance to closest stream and the CDCF were square-root transformed. All variables were standardised by their mean and standard deviation.

Modelling

Generalized linear mixed modelling was used as it performed better with our data than regression trees and artificial neural networks, based on the correct classification rate of presence–absence, the area under the curve of the receiver operating characteristic (ROC) plot and the Cohen's Kappa (see Model evaluation). Regression trees and artificial neural networks represent alternatives to linear modelling that relax some common assumptions such as normality of residuals, linear relationship and no correlations between predictors (Manel et al. 1999; Ozesmi and Ozesmi 1999; Guisan and Zimmermann 2000). Their benefits have, however, received little support in species distribution modelling of some taxa such as birds (e.g., Manel et al. 1999). The patch was incorporated as a random factor in order to account for the lack of independence between sites within each forest patch, with random variation in

Table 1 Variables considered in the three approaches considering either factors of local habitat, factors of metapopulation dynamics (patch size and isolation), or their combination to explain robin occurrence in forest patches

Approach	Full model variables
Local habitat only	CanH, SecCanH, TallTreeD, SmallTreeD, DBH, VineD, USH, MinSlope, Elev, DistToS, DistToE
Metapopulation factors	P_Area, CDCF, IFPC
Habitat and metapopulation factors	CanH, SecCanH, TallTreeD, SmallTreeD, DBH, VineD, USH, MinSlope, Elev, DistToS, DistToE, P_Area, P_Shape, CDCF, IFPC

CanH Tall canopy height, *SecCanH* Secondary canopy height, *TallTreeD* Tall tree density, *SmallTreeD* Small tree density, *DBH* Diameter of tree trunks at breast height, *VineD* Vine density, *USH* Understory height, *MinSlope* Minimum slope, *Elev* Elevation, *DistToS* Distance to stream, *DistToE* Distance to edge, *P_Area* Patch area, *P_Shape* Patch shape, *CDCF* Cost distance to continuous forest, *IFPC* Index of functional patch connectivity

occupancy probability among patches assumed to be logit-normally distributed. The modelling was performed using the software R (R Development Core Team 2006), using the function `lmer` from the `lme4` package.

For each of the three approaches, a full model was first run with all the variables (Table 1). Variable selection was first performed by backward stepwise selection based on Akaike's information criterion (AIC), with lower AIC values indicating a more parsimonious model (Burnham and Anderson 2002). This selection algorithm was chosen as it is considered to perform better than the forward selection in presence of correlated predictors (Harrell 2001). Forward stepwise selection was then performed on the best models to assess whether they could be improved.

Model evaluation

To assess the performance of the final models under each approach, a new dataset was first created for each model by leave-one-out cross-validation, where each observation was predicted from the best models calibrated with the remaining observations. The evaluation of the final models was then assessed on the cross-validated datasets using a ROC plot. The ROC plot represents the relationship between true-presences and false-presences for a range of threshold values classifying the probability of presence, and the area under the curve (AUC) represents a measure of overall accuracy (Fielding and Bell 1997). We also used the highest Cohen's Kappa (κ) that could be obtained on the whole range of possible cut-off values as an indicator of each model's performance. The Kappa statistic has been proposed to evaluate the

predictive success in relation to chance expectation (Cohen 1960; Fielding and Bell 1997), and can be used to classify model agreement as poor ($\kappa < 0.4$), good ($0.4 \leq \kappa < 0.75$), or excellent ($\kappa \geq 0.75$), following Landis and Koch (1977).

An increasing body of literature highlights biases induced by spatial autocorrelation of data, resulting in the effects of habitat variables being overestimated (Legendre 1993; Keitt et al. 2002; Betts et al. 2006). The presence of spatial autocorrelation in the models was assessed from the semivariograms of the residuals of each model, using the package `GeoR` in R (Ribeiro and Diggle 2001; available at <http://www.r-project.org>). Semivariograms are plots of the semivariance against lag distance. The semivariance is the halved average of squared differences between all points that are separated by lag distance t . If the compared points are increasingly different as t increases, the semivariance increases, and conversely, the semivariance decreases with the similarity of the compared points. The significance of spatial autocorrelation from the semivariograms was assessed visually by calculating an envelope obtained from 100 Monte-Carlo simulations, so that any semivariance outside the envelope indicates a significant autocorrelation at $\alpha = 0.01$. For each simulation, the data values were randomly allocated to the spatial locations, and the envelope therefore represents the variation in the semivariance of the residuals expected solely by chance in absence of spatial autocorrelation (Ribeiro and Diggle 2001).

Comparison of isolation indices

We compared the three calculated indices of patch isolation by running the backward then forward

stepwise selection on the full combined model with Euclidean distance to the closest continuous forest instead of the CDCF, and either the Euclidean distance to the nearest neighbouring patch or the proximity index instead of the IFPC. The performance of the resulting two best models was then compared with the best one of the combined approach in which patch isolation was described by IFPC and CDCF.

Results

Robins were recorded as present in 127 (32%) out of 400 sampled sites, and in 33 (45%) out of 74 forest patches (Fig. 1).

Models selected under the three approaches

The approach combining both habitat and metapopulation factors produced the best model in terms of AIC, AUC, Kappa, correct classification rate, and

sensitivity values (Table 2). The model including only patch size and isolation (i.e., metapopulation factors) had a lower AIC. However, both of these models are considered excellent based on Hosmer and Lemeshow's (2000) criteria for AUC, good (Landis and Koch 1977) criteria for Kappa, and had high (>0.8) correct classification rates. Patch isolation, as measured by IFPC and CDCF, is sufficient to explain most of the variation in robin presence–absence as indicated by the good predictive power of the model including only these variables. In contrast, the approach considering only habitat factors led to a poor model based on all measures of model evaluation. Furthermore, the residuals of this model showed some spatial autocorrelation at lag 500 m, in contrast to those including metapopulation factors (Fig. 2).

The best model indicated that robins are most likely to be present in larger patches (P_Area) that are well connected to surrounding patches (IFPC) and to the surrounding continuous forest (CDCF; Table 3). The habitat factors that increased probability of

Fig. 1 Presence–absence of North Island robins in forest fragments in an agricultural landscape of central North Island in New Zealand. The inset shows the location of the study area in New Zealand

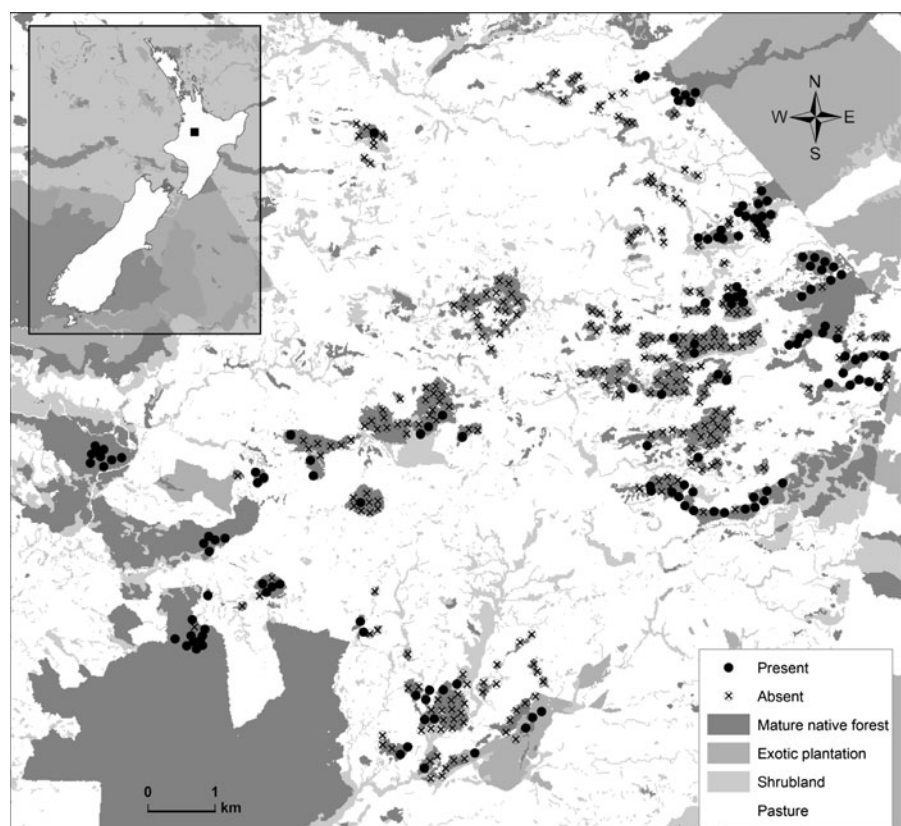


Table 2 Comparison of the best selected models under each of the three approaches considering either factors of local habitat, factors of metapopulation dynamics (patch size and isolation), or a combination of them, with isolation defined by either our

index of functional patch connectivity (IFPC), Euclidean distance to nearest neighbouring patch (NN), or Proximity (Prox), to explain robin occurrence in forest patches

Approach	AIC	AUC	Kappa	CCR	Sens.	Spec.	Spatial autocorr.
Habitat factors only	388.9	0.697	0.307	0.682	0.606	0.718	Yes
Metapopulation factors only	370.2	0.812	0.534	0.810	0.591	0.912	No
Combined with IFPC	359.3	0.828	0.546	0.810	0.638	0.890	No
Combined with NN	378.4	0.769	0.492	0.792	0.567	0.897	Yes
Combined with Prox	370.6	0.793	0.468	0.782	0.551	0.890	No
Patch isolation only	370.7	0.807	0.492	0.793	0.567	0.897	No

The fit and performance of the model including only patch isolation (IFPC + CDCF) is also presented

AIC Akaike's Information Criterion, *AUC* area under the ROC curve, *Kappa* Cohen's Kappa statistic, *CCR* Correct classification rate, *Sens.* sensitivity, *Spec.* specificity, *Spatial autocorr.* spatial autocorrelation of the residuals

occupancy were high understory (USH), tall canopy (CanH), and low density of regenerating trees (SmallTreeD).

By examining the last steps of the backward selection process based on AIC, several models had ΔAIC values < 2 (i.e., within two units of the best model), and can therefore be considered as reasonable alternative models (Burnham and Anderson 2002). Model averaging using all models with $\Delta AIC < 2$ suggested that robins were more likely to be present in flat areas (MinSlope; Table 4), and away from the forest edge (DistToE).

From the comparison of the best models including both habitat and metapopulation factors but differing in their indices to define patch isolation, the approach in which isolation is defined by IFPC and CDCF outperformed those with indices based on Euclidean distances in terms of AIC, AUC, Cohen's Kappa, and correct classification rate (Table 2). Moreover, the approach in which isolation is measured as the Euclidean distance to the nearest neighbouring patch led to a model in which residuals showed some level of spatial autocorrelation (Fig. 2).

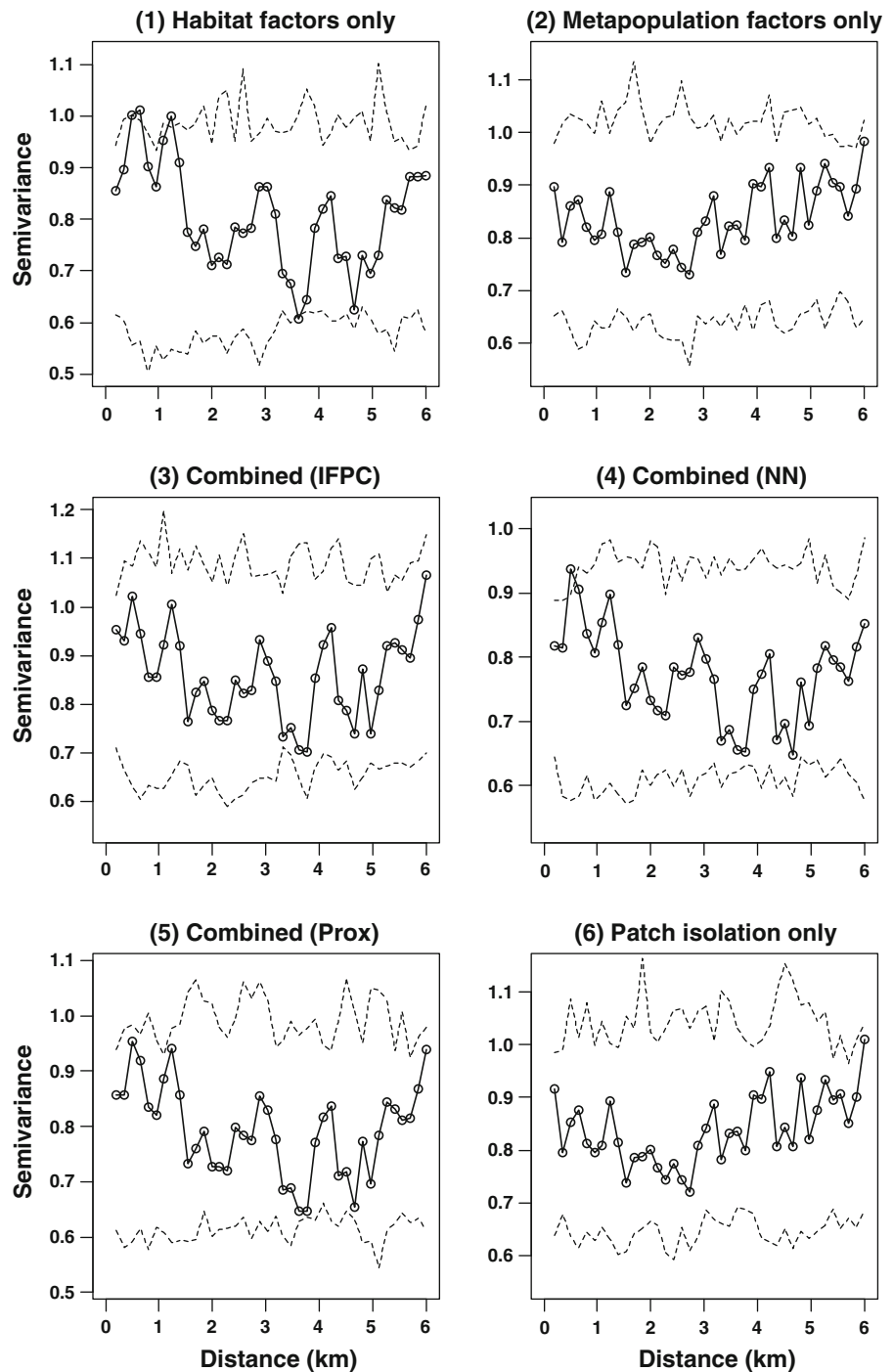
Discussion

Our results clearly showed that the consideration of metapopulation dynamics, by incorporating patch size and functional connectivity, greatly improved the accuracy of the models of robin presence–absence in the fragmented landscape we studied. Robin occurrence can even be accurately predicted with a simple

model including only patch size and isolation. The further consideration of habitat factors only led to a slight increase in model accuracy and predictive power. Conversely, only accounting for habitat factors led to a poor model, with low predictive accuracy. Furthermore, the spatial autocorrelation of residuals found under the approach considering only habitat factors disappeared when patch isolation was included in the model, indicating that the lack of dependence among sites was induced by species movements. Spatial autocorrelation can introduce some bias in the analysis (Lichstein et al. 2002) and more complicated models such as autologistic regression are often required to cope with this problem (Klute et al. 2002; Wintle and Bardos 2006), but controlling for the processes inducing this spatial autocorrelation should be preferred when possible and is likely to improve model fit and accuracy.

The importance of functional patch connectivity in explaining robin presence–absence is consistent with our research on dispersal of juvenile robins in the same landscape (Richard and Armstrong 2010). Juveniles were found to disperse preferentially in woody vegetation and unlikely to cross gaps in forest cover of more than 110 m. With pasture acting as a dispersal barrier, it is sensible to model patch isolation using a functional definition, based on cost distances instead of Euclidean distances. Indices based on Euclidean distances ignore the structure of the matrix between patches, which often influences species movements (Ricketts 2001), and are unlikely to reflect the true movements between patches. As expected, the approach using IFPC and

Fig. 2 Semivariograms of the residuals of the best models to explain robin presence–absence under three modelling approaches, considering only habitat factors (1), only factors of metapopulation dynamics (2), or a combination, with isolation defined either by our index of functional patch connectivity (3), the Euclidean distance to nearest neighbouring patch (4), or the proximity index (5). The semivariogram of the model including only patch isolation is also represented (6). The dashed lines represent the envelope obtained from 100 Monte Carlo simulations. Any point outside this envelope therefore represents a significant spatial autocorrelation at $\alpha = 0.01$



CDCF to define patch isolation led to a much better model than when using the distance to the nearest neighbouring patch and the index of proximity, both of which are based on Euclidean distances (Table 2).

The limitation of movement between patches can cause the species to be absent in good quality habitat patches. This result is expected based on metapopulation theory (Hanski and Gaggiotti 2004) but is curiously overlooked in many studies looking at

Table 3 Best generalised linear mixed models under each of the three approaches to explain the presence–absence of North Island robins in forest fragments

Approach	Factors	Coefficients	S.E.
Local habitat only	USH	0.577	0.184
	Elev	0.451	0.227
	CanH	0.421	0.190
	SmallTreeD	−0.319	0.215
Metapopulation factors only	CDCF	−0.795	0.270
	IFPC	0.765	0.320
	P_Area	0.341	0.219
Habitat and metapopulation factors	IFPC	0.893	0.299
	CDCF	−0.781	0.266
	USH	0.500	0.175
	CanH	0.444	0.187
	SmallTreeD	−0.372	0.212

The factors included in the three final models are shown, along with their estimates (change in logit of occupancy probability with a one unit increase in the value of the factor) and their standard errors. Standardised variables were used to allow direct comparison of coefficients. See Table 1 for explanation of the factors

Table 4 Parameter coefficients of the model obtained from averaging all models within two units of AIC from the best model during stepwise model selection to explain robin occurrence inhabiting forest patches in an agricultural landscape of central North Island in New Zealand

Factors	Coefficients
IFPC	0.867
CDCF	−0.801
USH	0.497
CanH	0.400
SmallTreeD	−0.285
MinSlope	−0.106
DistToE	0.048

species occurrence (e.g., Cowley et al. 2000; Fleishman et al. 2003; Whittingham et al. 2007). Omission of metapopulation factors may introduce biases in the analysis of the relationship between habitat and species occurrence. For example, consideration of habitat factors alone leads to the conclusion that robins are more likely to be present at higher elevation, which could be interpreted as a preference of robins for colder temperature, suggesting they are sensitive to global warming. However, this is due to elevation being correlated with connectivity, and the

effect disappears when connectivity is accounted for (Table 3).

We defined patch isolation at two different scales, isolation from neighbouring patches and from the surrounding continuous forest, as we suspected that the major forest near the study area would act as a source of immigrants, or as a “continent” following MacArthur and Wilson (1967). Patch isolation from putative sources (i.e., from major forest areas) was indeed a good predictor of robin presence–absence, indicating that the study area benefits from the immigration of individuals from surrounding habitats. The nearest forests are mainly exotic plantations of *Pinus radiata* where robins are present in locally high densities. However, a study on robin vital rates in this habitat showed extremely low productivity in robins inhabiting pine forests (McArthur, unpub.). It is therefore more likely that the immigrants in the study area originate from Pureora Forest Park, where populations of predators such as rats, possums and stoats, considered as the main causes of the decline of native species in New Zealand (Holdaway 1999), are regularly controlled by poison and trapping operations. Pureora Forest Park is located only 10 km to the east and is well connected to the study area by the exotic forests, without major gaps between forests. Furthermore, robin juveniles followed by radiotracking have been recorded moving total distances up to 20 km although the Euclidean distances from start to end point are a small fraction of this due to constraints imposed by fragmentation (Richard 2007). However, these plantations are due to be felled, which may provoke the local extinction of robins in the study area without the continued immigration of individuals from Pureora Forest Park.

Our results suggest that North Island robins are preferentially found in mature forests, characterized by a tall canopy and a lower density of regenerating trees, and in habitats with tall understory, suggesting a negative impact of grazing animals such as goats, pigs, rabbits, cows and sheep, all introduced by humans during colonisation (Table 3). A sparse or nonexistent understory can potentially be associated with a low diversity in insect communities and perhaps lower food availability for robins (Didham et al. 2009) as their nest survival is positively related to invertebrate biomass (Boulton et al. 2008).

Robins were also found preferentially in larger forest patches (Tables 3 and 4), and similar area

effects have been found in numerous fragmentation studies (e.g., Helzer and Jelinski 1999; Connor et al. 2000; Castellón and Sieving 2006). The mechanisms underlying such area effects are usually unclear, as large patches could be more likely to be occupied because they are less susceptible to chance extinction (“metapopulation paradigm”), because the smaller amount of edge means they have higher average habitat quality (“habitat paradigm”), or other reasons. We attempted to separate these effects by controlling for distance to edge and for variables potentially measuring local habitat quality more directly. However, without the certainty of controlling for all habitat factors affecting robins’ presence–absence, the effect of patch area we found might still be partially due to some habitat factors we did not record. The underlying ecological mechanisms of patch area are yet to be clarified if one wants to lessen the impact of habitat loss and fragmentation on biodiversity. However, the model only including patch isolation (IFPC and CDCF; Table 2) performed almost as well as the best model which also considered patch area, indicating that patch area is not a major factor in explaining the presence–absence of robins.

It is fundamental to distinguish the relative effects of habitat fragmentation on metapopulation dynamics and habitat quality if one wants to rescue many species from extinction (Armstrong 2005). This can potentially be achieved by analysing the presence–absence of organisms in fragmented landscapes, but requires taking into account the dangerous associated pitfalls. It should be noted however that the effect of habitat characteristics on species presence–absence does not necessarily measure habitat quality (Armstrong 2005), which should be ideally measured from the analysis of vital rates (survival and reproduction). Moreover, the importance of patch isolation does not necessarily indicate that landscape connectivity is beneficial to the metapopulation (Simberloff et al. 1992), and its effect on species persistence needs to be assessed using spatially-explicit population models (Carroll 2006).

This study clearly highlights the need to integrate landscape ecology in habitat models. By ignoring the factors of metapopulation dynamics and landscape connectivity, spurious relationships may arise and lead to erroneous interpretations and management recommendations. Patch isolation should be modelled

by using indices accounting for the dispersal ecology of species and the structure/composition of landscapes to fully appreciate the importance of habitat loss and fragmentation.

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References

- Anderson AJ (1991) The chronology of colonization in New Zealand. *Antiquity* 65:767–795
- Andren H (1995) Effects of landscape composition on predation rates at habitat edges. In: Hansson L, Fahrig L, Merriam G (eds) *Mosaic landscapes and ecological processes*. Chapman & Hall, London, UK, pp 225–255
- Armstrong DP (2005) Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. *Conserv Biol* 19:1402–1410
- Armstrong DP, Raeburn EH, Lewis RM, Ravine D (2006) Modeling vital rates of a reintroduced New Zealand robin population as a function of predator control. *J Wildl Manage* 70:1028–1036
- Bell BD (1986) The conservation status of New Zealand wildlife. New Zealand Wildlife Service, Dept. of Internal Affairs, Wellington, New Zealand
- Betts M, Diamond A, Forbes G, Villard M (2006) The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecol Model* 191:197–224
- Bock CE, Jones ZF (2004) Avian habitat evaluation: should counting birds count? *Front Ecol Environ* 2:403–410
- Boulton RL, Richard Y, Armstrong DP (2008) Influence of food availability, predator density and forest fragmentation on nest survival of New Zealand robins. *Biol Conserv* 141:580–589
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449
- Burke DM, Nol E (1998) Influence of food abundance, nest-site habitat, and forest fragmentation on breeding oven-birds. *Auk* 115:96–104
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York, USA
- Carroll C (2006) Linking connectivity to viability: insights from spatially explicit population models of large carnivores. In: Crooks KR, Sanjayan MA (eds) *Connectivity conservation*. Cambridge University Press, Cambridge, UK, pp 369–389

- Castellón TD, Sieving KE (2006) Landscape history, fragmentation, and patch occupancy: models for a forest bird with limited dispersal. *Ecol Appl* 16:2223–2234
- Caughley G (1994) Directions in conservation biology. *J Anim Ecol* 63:215–244
- Chalfoun AD, Thompson FR III, Ratnaswamy MJ (2002) Nest predators and fragmentation: a review and meta-analysis. *Conserv Biol* 16:306–318
- Clubb S (2003) Territory choice of reintroduced North Island robins (*Petroica australis longipes*) in a predator controlled forest reserve in New Zealand. M.Sc. thesis, Napier University, Edinburgh, Scotland
- Cohen J (1960) A coefficient of agreement for nominal scales. *Educ Psychol Meas* 20:37–46
- Connor EF, Courtney AC, Yoder JM (2000) Individuals-area relationships: the relationship between animal population density and area. *Ecology* 81:734–748
- Cowley MJR, Wilson RJ, Leon-Cortes JL, Gutierrez D, Bulman CR, Thomas CD (2000) Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *J Appl Ecol* 37:60–72
- Didham RK, Barker GM, Costall JA, Denmead LH, Floyd CG, Watts CH (2009) The interactive effects of livestock exclusion and mammalian pest control on the restoration of invertebrate communities in small forest remnants. *N Z J Zool* 36:135–163
- Doak P (2000) The effects of plant dispersion and prey density on parasitism rates in a naturally patchy habitat. *Oecologia* 122:556–567
- Doebeli M, Ruxton GD (1998) Stabilization through spatial pattern formation in metapopulations with long-range dispersal. *Proc R Soc Lond Biol Sci* 265:1325–1332
- Ewers RM, Kliskey AD, Walker S, Rutledge D, Harding JS, Didham RK (2006) Past and future trajectories of forest loss in New Zealand. *Biol Conserv* 133:312–325
- Farina A (1998) Principles and methods in landscape ecology. Chapman & Hall, London, UK
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 24:38–49
- Fleishman E, Mac Nally R, Fay JP (2003) Validation tests of predictive models of butterfly occurrence based on environmental variables. *Conserv Biol* 17:806–817
- Gobeil J-F, Villard M-A (2002) Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98:447–458
- Goodwin BJ, Fahrig L (2002) How does landscape structure influence landscape connectivity? *Oikos* 99:552–570
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186
- Gustafson EJ, Parker GR (1994) Using an index of habitat patch proximity for landscape design. *Landsc Urban Plann* 29:117–130
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Hanski I, Gaggiotti OE (2004) Metapopulation biology: past, present, and future. In: Hanski I, Gaggiotti OE (eds) *Ecology genetics and evolution of metapopulations: standard methods for inventory and monitoring*. Elsevier, London, UK, pp 3–22
- Hanski I, Alho J, Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* 81:239–251
- Harrell FE (2001) *Regression modelling strategies: with application to linear models, logistic regression, and survival analysis*. Springer, New York, USA
- Harrison S, Bruna E (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22:225–232
- Haynes KJ, Cronin JT (2006) Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. *Oikos* 113:43–54
- Heather BD, Robertson HA (2000) *The field guide to the birds of New Zealand*. Viking, Auckland, New Zealand
- Helzer CJ, Jelinski DE (1999) The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecol Appl* 9:1448–1458
- Higgins PJ, Peter JM (2002) *Petroica australis*, New Zealand robin. In: Higgins PJ, Peter JM (eds) *Handbook of Australian, New Zealand, and Antarctic Birds*. Vol. 6: Pardalotes to Shrike-Thrushes. Oxford University Press, Melbourne, Australia, pp 706–725
- Holdaway RN (1999) Introduced predators and avifaunal extinction in New Zealand. In: McPhee RD (ed) *Extinctions in near time*. Kluwer Academic/Plenum, New York, USA, pp 189–238
- Hosmer DW, Lemeshow S (2000) *Applied logistic regression*, 2nd edn. Wiley, New York, USA
- Keitt TH, Bjørnstad ON, Dixon PM, Citron-Pousty S (2002) Accounting for spatial pattern when modeling organism-environment interactions. *Ecography* 25:616–625
- Klute DS, Lovallo MJ, Tzilkowski WM (2002) Autologistic regression modeling of American woodcock habitat use with spatially dependent data. In: Scott JM, Heglund PJ, Morrison ML, Haufler JB, Raphael MG, Wall WA, Samson FB (eds) *Predicting species occurrences*. Island Press, Washington, DC, pp 335–343
- Landis JR, Koch GC (1977) The measurement of observer agreement for categorical data. *Biometrics* 33:159–174
- Lawton JH, Woodroffe GL (1991) Habitat and the distribution of water voles: why are there gaps in species range? *J Anim Ecol* 60:79–91
- Leathwick JR, Wilson G, Rutledge D, Wardle P, Morgan F, Johnston K, McLeod M, Kirkpatrick R (2003) *Land environments of New Zealand*. Auckland, New Zealand
- Legendre P (1993) Spatial autocorrelation: problem or new paradigm? *Ecology* 74:1659–1673
- Lichstein JW, Simons TR, Shiner SA, Franzreb KE (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecol Monogr* 72:445–463
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA
- Manel S, Dias JM, Ormerod SJ (1999) Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. *Ecol Model* 120:337–347
- Moilanen A, Hanski I (1998) Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79:2503–2515

- Ozesmi SL, Ozesmi U (1999) An artificial neural network approach to spatial habitat modelling with interspecific interaction. *Ecol Model* 116:15–31
- Paton PWC (1994) The effect of edge on avian nest success: how strong is the evidence? *Conserv Biol* 8:17–26
- Potter MA (1990) Movement of North Island Brown Kiwi (*Apteryx australis mantelli*) between forest remnants. *N Z J Ecol* 14:17–24
- Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132:652–661
- Reed DH (2004) Extinction risk in fragmented habitats. *Anim Conserv* 7:181–191
- Ribeiro PJ Jr, Diggle PJ (2001) geoR: a package for geostatistical analysis. *R-NEWS* 1:15–18
- Richard Y (2007) Demography and distribution of the North Island robin (*Petroica longipes*) in a fragmented agricultural landscape of New Zealand. Ph.D. thesis, Massey University, Palmerston North, New Zealand
- Richard Y, Armstrong DP (2010) Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. *J Appl Ecol* 47:603–610
- Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *Am Nat* 158:87–99
- Robertson CJR, Hyvönen P, Fraser MJ, Pickard CR (2007) Atlas of bird distribution in New Zealand, 1999–2004. The Ornithological Society of New Zealand, Inc., Wellington, New Zealand
- Rushton SP, Barreto GW, Cormack RM, Macdonald DW, Fuller R (2000) Modelling the effects of mink and habitat fragmentation on the water vole. *J Appl Ecol* 37:475–490
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 5:18–32
- Sih A, Jonsson BG, Luikart G (2000) Habitat loss: ecological, evolutionary and genetic consequences. *Trends Ecol Evol* 15:132–134
- Simberloff D, Farr JA, Cox J, Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? *Conserv Biol* 6:493–504
- Smart SM, Furbank LG, Bunce RG, Watkins JW (2000) Quantifying changes in abundance of food plants for butterfly larvae and farmland birds. *J Appl Ecol* 37:398–414
- R Development Core Team (2006) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org>
- Van Horne B (1983) Density as a misleading indicator of habitat quality. *J Wildl Manage* 47:893–901
- Van Teeffelen AJA, Cabeza M, Moilanen A (2006) Connectivity, probabilities and persistence: comparing reserve selection strategies. *Biodivers Conserv* 15:899–919
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277:494–499
- Whittingham MJ, Krebs JR, Swetnam RD, Vickery JA, Wilson JD, Freckleton RP (2007) Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecol Lett* 10:25–35
- Winfree R, Dushoff J, Crone EE, Schultz CB, Budny RV, Williams NM, Kremen C (2005) Testing simple indices of habitat proximity. *Am Nat* 165:707–717
- Wintle BA, Bards DC (2006) Modeling species-habitat relationships with spatially autocorrelated observation data. *Ecol Appl* 16:1945–1958