Strong influence of local habitat structure on mammals reveals mismatch with edge effects models

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Abstract

Context: What determines mammal occurrence across wildland-urban edges? A better understanding of the variables involved will help update edge effects theory and improve our ability to conserve biota in urbanizing landscapes.

Objectives: For the first time, we tested whether the occurrence of mammals across urban-forest edges and forest interiors was best predicted by: (1) edge variables (i.e. edge type and distance to an urban boundary), (2) local habitat structure (e.g. proportion of understory cover), or (3) edge variables after accounting for local habitat structure.

Methods: Using 77 camera stations in south-eastern Australia, we quantified the factors influencing the occurrence of five native mammals (brown antechinus, bush rat, common brushtail possum, black wallaby and long-nosed bandicoot) and three non-native mammals (red fox, cat, and dog).

Results: The occurrence of most native and non-native mammals was best predicted by local habitat structure rather than by edge variables. Although edge variables had effects on most species occurrences, local habitat structure outweighed the impacts of edge effects.

Conclusions: Our findings are important for management and urban planning as they suggest that local-scale management of habitat and habitat retention at urban edges will mitigate urban impacts on fauna. Our work reveals a critical mismatch in the spatial scale of predictive variables commonly used in edge effects models (edge types and distance to a boundary) compared with the smaller scale of local habitat variables, which underlie most species occurrence. We

emphasize the need to consider heterogeneity within patches in predictive frameworks of edge effects.

Key-words: edge contrast, habitat boundaries, mammal occurrence, residential areas, spatial scale, urbanization, vertically-oriented camera trapping.

Introduction

The creation and expansion of urban areas increases the area and number of edge environments by modifying and fragmenting natural landscapes (Radeloff et al 2005; Brearley et al 2010; Groffman et al 2014). Edges created by urban development are not uniform because residential development occurs at different housing densities (Sushinsky et al 2013). Therefore, urban areas need to be thought not as homogeneous hostile environments, but rather as a collection of patches of different quality for biodiversity (Lindenmayer and Fischer 2006; Do et al 2014; Groffman et al 2014). As a result, species are unlikely to respond uniformly to the variety of edges generated by urban development (Ikin et al 2013; Forman 2014; Villaseñor et al 2014).

Species responses across edges can be influenced by *edge variables* or by *local habitat* characteristics along an edge (Lidicker 1999; Kristan et al 2003; Ikin et al 2014). *Edge variables* are those that are directly associated with the juxtaposed patches that generate an edge, such as distance to a boundary (Harper et al 2005) and edge type (Ries et al 2004). In urban landscapes, distance to an urban boundary (Kristan et al 2003; Ordenana et al 2010) and edge types classified by the housing density at an edge (Hodgson et al 2007; Villaseñor et al 2014) can affect responses by species. Species also can respond to *local habitat* characteristics (Brearley et al 2010). Although *local habitat* characteristics can be driven by edge effects (Lidicker 1999; Kristan et al 2003; Laurance et al 2011), *local habitat* characteristics also may vary independently of the edge and therefore could explain additional variation to that associated with an edge.

A key question relevant to the management and planning of urban areas is therefore: What are the main factors influencing species responses across habitat edges? Despite there being abundant research into edge effects (reviewed by Murcia 1995; Ries et al 2004; Harper et al 2005; Vetter et al 2013), the "quantification of the specific mechanisms that underlie observed edge patterns is still lacking for most systems" (Wimp et al 2011; p. 869). Furthermore, studies of ecological processes across edges have usually been restricted to one side of a boundary (e.g. Harper et al 2005; Fonderflick et al 2013), have focused on forested remnants adjacent to pastures or crops (e.g. Forman 1995; Harper et al 2005), and been conducted on a small spatial scale (but see Ewers and Didham 2008; Laurance et al 2011).

Our study is the first to address these key knowledge gaps by measuring the response of mammal species in a mosaic landscape of forests and urban areas with varying housing densities. This study is needed because the variables at habitat edges that ground-dwelling mammals respond to remain unknown (Mills 1995; Kristan et al 2003; Ries et al 2004; Porensky 2011; Prevedello et al 2013). We investigated which variables best predicted mammal occurrence across urban-forest edges and forest interiors. In particular, we posed the following three questions:

(1) How well do *edge variables*, such as the housing density at the urban-forest edge and distance to the urban boundary, predict individual species occurrences?

(2) How well do *local habitat variables*, such as local habitat structure, predict individual species occurrences? And,

(3) How well do *edge variables, after accounting for local habitat effects*, predict individual species occurrences?

Given the rapid and accelerating expansion of urban areas into forested areas (Stein et al 2012; Wood et al 2014), further understanding of potential changes to biodiversity in wildland-urban interfaces is required to guide management and urban planning. The findings of this study will allow managers and urban planners to make informed decisions when evaluating both impacts of development on wildlife and mitigation and restoration strategies. For instance, if *local habitat variables* are the main predictors of animal response, animal populations are likely to respond to local management such as restoration (Kristan et al 2003). If *edge variables* have a greater impact, local-scale habitat management might be unsuccessful in conserving animal populations, whereas decisions on the design and housing densities in the urban mosaic would have a greater effect on biodiversity. We draw on our results to: (1) inform ecologically sustainable urban development and (2) improve existing conceptual models for predicting the response of species to habitat edges.

Methods

Study area

Our study was located on the south coast of New South Wales, south-eastern Australia (Figure 1A). It encompasses an area between the towns of Callala Bay (34°59'S 150°43'E) and Berrara (35°12'S 150°33'E), and covers approximately 500 km^2. The climate in the region is

characterized by mild summers (mean maximum temperature= 24°C), mild winters (mean maximum temperature=16.5°C), and an annual rainfall of ~1,000 mm that is distributed evenly throughout the year (Bureau of Meteorology 2013).

Our study area is dominated by native forests of the genus *Eucalyptus*. Natural vegetation and wetlands cover 81.4% of the landscape, followed by urban areas (13.4%) and a small percentage of other land uses (e.g. grazing, cropping, mining; 5.3%) (Emery 2010). We selected this landscape to reduce landscape-scale variation across sites. High human population growth and an increasing demand for holiday houses are triggering further clearing of vegetation for urban development (State of New South Wales 2007). This land use change is creating urban areas of different housing densities interspersed with natural areas such as national parks and reserves.

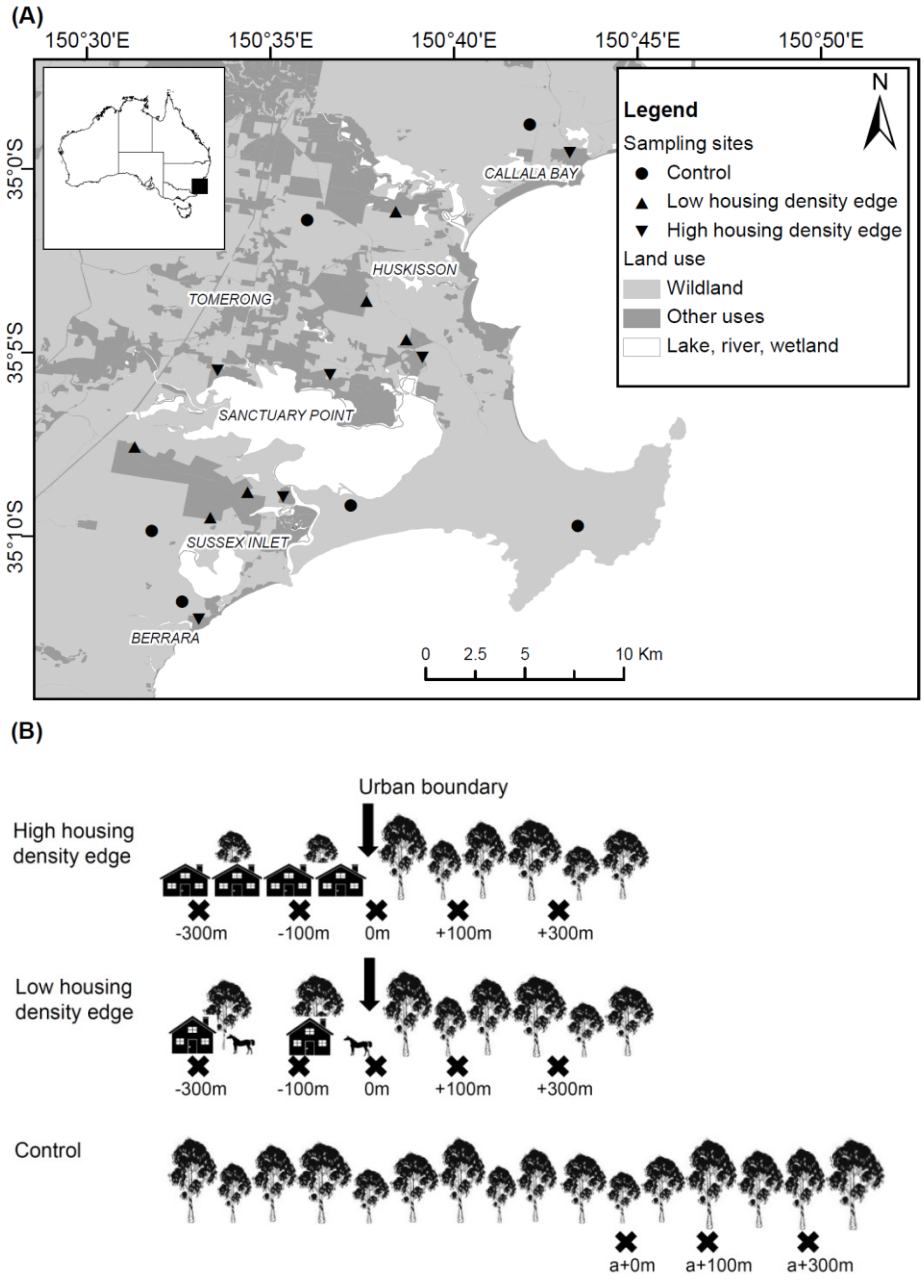


Figure 1. (A) Study area and sites of mammal surveys in south-eastern Australia. (B) Diagram of the station placement for camera trapping in study sites. At each of the high and low housing density edge a station was established at -300 m, -100 m, 0 m, +100 m, and +300 m from the urban boundary. Control sites included camera stations at 0 m, +100 m, and +300 m from a random point ("a") further than 500 m away from other land use. Arrows indicate the urban boundary.

Site selection

To study the effect of both housing density at the urban-forest edge and distance to the urban boundary on ground-dwelling mammals, we selected 18 sites: six urban-forest edges with high housing density, six urban-forest edges with low housing density and six forested controls (Figure 1A) (for a study on arboreal marsupials, see Villaseñor et al 2014). To select sites, we first identified urban cover with high and low housing densities in a land use shapefile (Emery 2010) in ArcGIS 10 (ESRI). Residential zones dominated by single storey houses (average lot size: 0.06 ha) represented high housing density, whereas rural residential zones with allotments from 0.2 to 16 ha in size represented low housing density. Urban boundaries adjacent to large areas of forest (i.e. forest extending beyond 600 m from the urban boundary) were identified as potential sites; and a subset of six sites was selected randomly in each housing density (i.e. high and low). Six control sites were selected randomly in large forested areas at least 0.5 km away from urban or other land uses, but within 8 km of an urban-forest edge site.

Surveys of ground-dwelling mammals

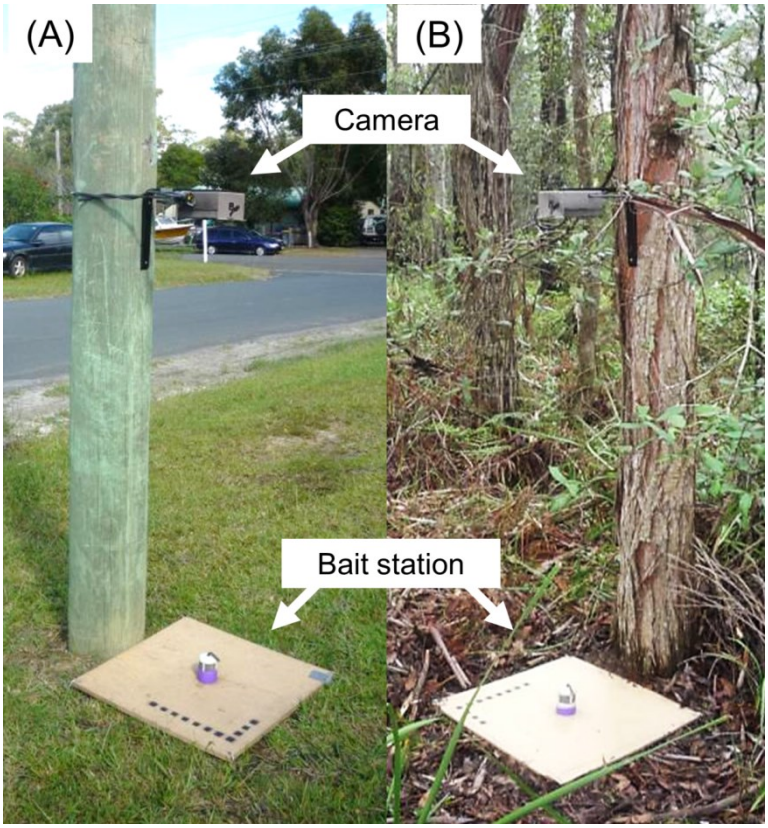
Between December 2012 and March 2013, we deployed infrared flash cameras at 77 stations within our 18 sites (Bushnell HD trophy cam, Trailcampro, USA). At each urban-forest edge site, we placed one camera at the urban boundary (distance to the urban boundary: $D = 0$ m), two cameras from the urban boundary into urban interior ($D = -100$ m, -300 m), and two cameras from the urban boundary into forest interior ($D = +100$ m, +300 m) (Figure 1B). At each control site (>0.5 km from an urban boundary or other land use), we established three cameras with the

same spacing as those located from the urban boundary into forest ($D = a + 0$ m, $D = a + 100$ m, $D = a + 300$ m, where a was a random point in each control site) (Figure 1B). The distance to the closest urban boundary for each camera in control sites was calculated using ArcGIS 10 (mean nearest distance from an urban boundary ± se = 1470 m ± 217 m). Due to a resident's concern about privacy issues, we were unable to install one camera in the high housing density treatment (D = -100 m).

A common limitation in camera trap studies is reduced species identification due to poor background contrast (with infrared flash) and a small proportion of images capturing the full profile of the animal when cameras aim horizontally (Smith and Coulson 2012). We overcame these limitations by mounting each camera vertically (facing downwards) (De Bondi et al 2010) at approximately 1.4 m above the ground against a contrasting 30 cm x 30 cm wooden platform marked with a measuring scale to aid in species identification (Figure 2).

We lured animals within the camera's field of view using a bait station comprised of an 84 mm length of PVC pipe (50 mm diameter with stainless steel mesh incorporated, sealed at the top). Bait was placed inside each pipe that was sealed with a balloon at the open end and mounted flush on the wood platform (Figure 2). Two bait types were used at each camera to increase the likelihood of detecting both herbivores and carnivores. A bait comprising peanut butter, rolled oats and fennel seeds (Pereoglou et al 2013) was used for the first three days and then replaced with bait of canned fish and rolled oats which remained in place for a further three

days. That is, each camera remained at a station for six consecutive days with the camera activated for 24 hours a day.



175 Figure 2. Vertically-oriented cameras in (A) an urban area with high housing density and (B) a forested control. Cameras were aiming to a bait station on the ground, that included a bait inside a PVC pipe with a metal mesh incorporated, mounted on a woody platform with a scaled reference to aid in species identification.

180 Once triggered by movement, a camera took three consecutive pictures and then waited for 10 s before recording the next event. To avoid overexposed flash photos, we set the infrared LED flash to "low" and covered all LED lights but the two middle ones with a white masking tape (three rows of masking tape were pasted over the LED flash). Mammals recorded were

identified from file images at the species level, or genus when a species was not entirely clear, using reference books (Van Dyck and Strahan 2008; Menkhorst and Knight 2010). Species identification was cross-checked by an individual with extensive mammal trapping experience in the study area (C. MacGregor, The Australian National University).

Habitat surveys

At each camera station (n=77), we measured habitat structure using the point-intercept method (Floyd and Anderson 1987) along a 50 m transect (50 points) that extended 25 m either side of the cameras. At each point, spaced at 1 m intervals, we recorded the presence/absence of the following variables: grass, litter, bare ground, impervious surfaces (e.g. concrete, bitumen, paving), woody debris, understory vegetation (excluding grass <1 m tall) and projective foliage of overstory vegetation (ground covered by a vertical projection of overstory foliage). The proportion cover of each habitat variable was calculated by dividing the total number of intercepts by the total number of points (50) on each transect.

Data analyses

For each mammal detected in at least five camera stations, we examined separately the effects of both edge and habitat variables on the occurrence of individual mammal species at each camera station (n=77) and then examined the effect of edge variables after accounting for the effects of habitat variables on each mammal species. We did this by performing model selection on three different candidate sets of Generalized Linear Models (GLMs) that represented (1) edge effects,

(2) habitat effects and (3) edge effects after accounting for habitat effects. After model selection, (4) significant explanatory variables from the best models selected from steps 1-3 were fitted using Generalized Linear Mixed Models (GLMMs) to interpret variable coefficients and standard errors while accounting for the random effect of site (n=18). As some of the candidate models were unable to be fit with GLMMs due to insufficient data, we performed the model selection via GLMs (see Bates 2010). Since we are ignoring the spatial dependence at the site level, we expect to identify terms which might be rendered unimportant when we take the spatial dependence into account using GLMMs.

First, we modeled edge effects by exploring the relationship between housing density and distance to the urban boundary on the occurrence of each species by fitting Generalized Linear Models (GLMs) with a binomial distribution and logit link function. To facilitate the interpretation of the results, we scaled distance to the urban boundary by dividing by 100 m. Edge effects models included the effect of housing density (three levels: high housing density, low housing density and forested control) and distance to the urban boundary (in isolation, as an additive term or as an interaction term). Interactions were explored to determine whether distance (length) of the edge effect varied with different housing densities. We fitted linear and quadratic effects of distance, which allowed different functional forms of the effect of distance to the urban boundary (Fonderflick et al 2013). Thus, a set of nine candidate models was constructed for each species (Supporting Information Table S1A).

Second, we summarized variation in habitat structure among camera stations (i.e. proportion cover of grass, litter, bare ground, impervious surfaces, woody debris and projective foliage of overstory vegetation) with metric multidimensional scaling (MDS). Thus, we created a pairwise Euclidean distance matrix that represented dissimilarities between camera stations and used metric MDS to find the best-fitting two-dimensional representation for these (Mardia 1978). We then built a set of seven candidate GLMs for each species, which included the isolated and additive effect of the two axes from the MDS (as a summary of habitat structure) and the proportion cover of understory (Supporting Information Table S1B). The latter variable is often a strong predictor of the occurrence of several ground-dwelling animals (Catling and Burt 1995; Tomasevic and Estades 2008; Van Dyck and Strahan 2008).

Third, to test the effect of edge variables in predicting species occurrence after accounting for habitat effects, we built a habitat plus edge model set. To do this, each of the nine edge GLMs from step one (Supporting Information Table S1A) was added to the best habitat model predicting each species occurrence selected in step two (Supporting Information Table S1B). By combining models in this way, we were able to infer the extent to which edge effects on each species occurrence were explained by habitat effects (Smith et al 2009).

We selected the 'best' GLM from each candidate set (i.e. edge, habitat and habitat plus edge) using Bayesian Information Criterion (BIC) (Raftery 1995). Similar to Akaike's Information Criterion (AIC), models with lower BIC values are better supported by the data. We

preferred BIC over AIC corrected by small sample size (AICc) because a model selection using AICc selected over-parameterized models (i.e. models containing parameters for which our data had little support). For each species, we looked for evidence in support of differences between the best models and a null model that represented the null hypothesis. We interpreted differences in BIC between models of 0-2 as weak, 2-6 as positive, 6-10 as strong and >10 as very strong (Raftery 1995).

Finally, using predictive variables from our 'best' models for each mammal species, we predicted the individual effect of each explanatory variable on mammal occurrence using GLMMs with binomial family (logit link). Thus, for each of the best edge, habitat, and habitat plus edge models, we added site (n=18) as a random effect. GLMMs with site as a random effect (i.e. grouping variable) allowed us to account for potential spatial autocorrelation because of nesting of camera traps within individual sites (three to five camera stations were placed within each site). Therefore, we were able to evaluate the effects of variables of interest (fixed effects) while assuming spatial autocorrelation between observations from cameras within the same site (Dormann et al 2007). Five adaptive Gauss-Hermite quadrature points were used to evaluate the marginal integral in the fitted GLMMs, which provides a better approximation of the integral than the Laplace approximation (Bolker et al 2009). When data on species occurrence had complete separation problems, we fitted models using Firth's penalized-likelihood logistic regression (Meinhard et al 2010).

All statistical analyses were performed in R-3.0.1 (R Core Team 2013). We used the function *cmdscale* in the package "stats" for metric MDS, "glmulti" for model selection (Calcagno 2013), "lme4" to fit GLMMs (Bates et al 2014), "logistf" to perform Firth's penalized-likelihood logistic regression (Meinhard et al 2010), and "AICcmodavg" to obtain predicted values and standard errors from best models (Mazerolle 2013).

Results

We obtained 4419 images containing animals over 462 camera-trap nights (i.e. 77 camera stations x 6 nights per camera). Of these, 3990 or 90% of images detected a mammal. A total of 3891 or 98% of images containing a mammal was identified to species level. We recorded 12 species of mammals comprising 10 ground-dwelling mammals and two arboreal mammals (Figure 3, Supporting Information Table S2).

Eight mammal species were detected at ≥ 5 camera stations (Supporting Information Table S2). We were able to fit statistical models for five of the eight native mammal species recorded (i.e. brown antechinus (*Antechinus stuartii*), bush rat (*Rattus fuscipes*), common brushtail possum (*Trichosurus vulpecula*), black wallaby (*Wallabia bicolor*), and long-nosed bandicoot (*Perameles nasuta*)) and three of four non-native species (i.e. dog (*Canis lupus familiaris*), cat (*Felis catus*), and red fox (*Vulpes vulpes*)). For each of these species, we present models of edge effects, habitat effects, and edge effects after accounting for habitat effects (Supporting Information Table S3).

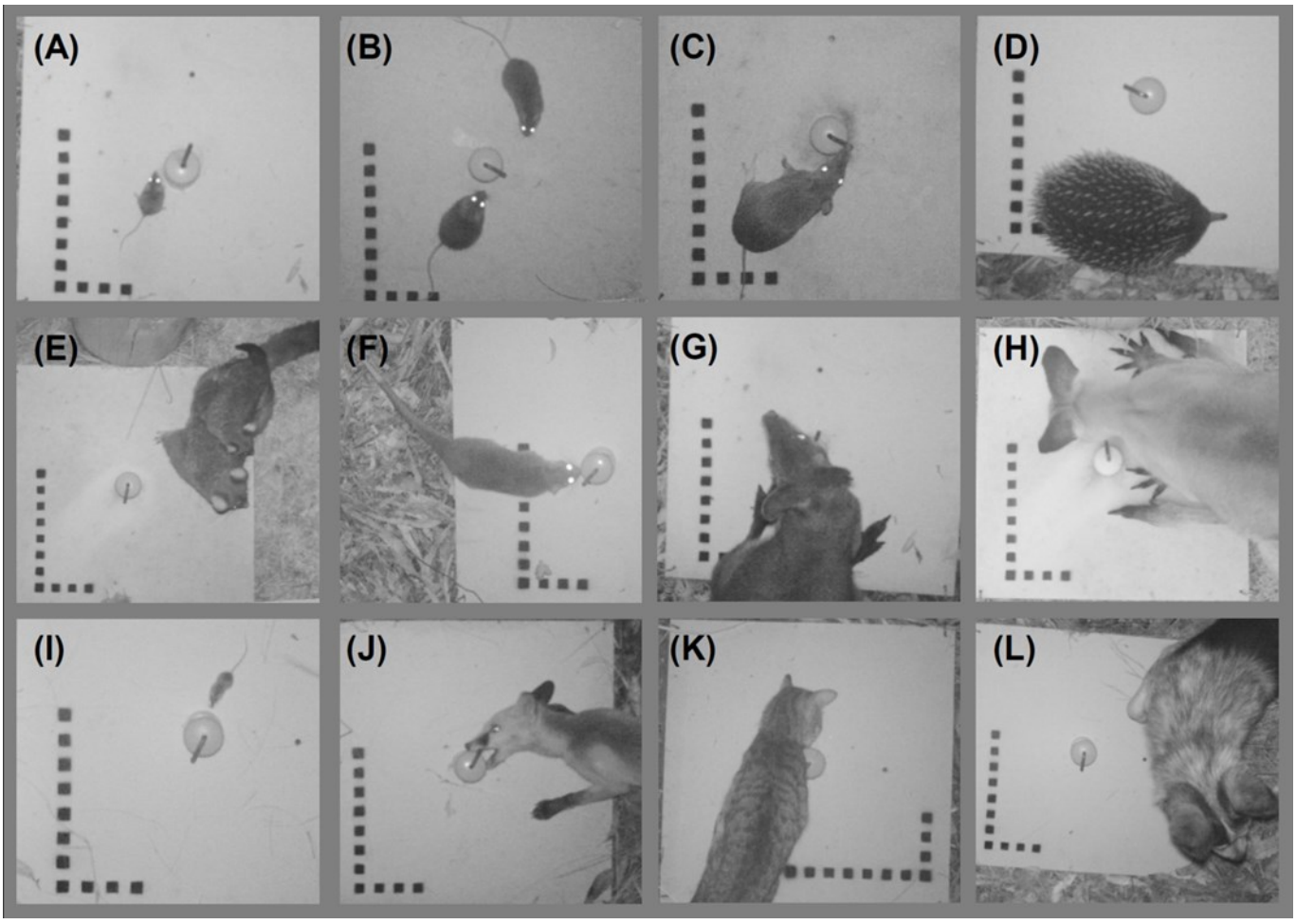


Figure 3. Photographs of mammal species recorded using 77 vertically-oriented cameras in south-eastern Australia. Native species included (A) brown antechinus, (B) bush rats, (C) long-nosed bandicoot, (D) short-beaked echidna, (E) common brushtail possum, (F) common ringtail possum, (G) black wallaby, and (H) eastern grey kangaroo. Non-native species included (I) house mouse, (J) red fox, (K) cat, and (L) dog.

Edge effects on mammals

No edge effect models were better than the null model for the black wallaby, long-nosed bandicoot and red fox (Table 1A). There was weak support for differences between the null model and housing density predicting bush rat occurrence, and the null model and distance to the boundary predicting common brushtail possum occurrence (ΔBIC<2). Positive support was

found for differences between the null model and the quadratic effect of distance to the urban boundary for brown antechinus occurrence, and the null model and the interaction between housing density and distance to the urban boundary for cat occurrence (ΔBIC>2) (Table 1A).

There was strong support for differences between the null model and the effect of distance to the urban boundary for dog occurrence (ΔBIC>6) (Table 1A).

Table 1. Effects of (A) edge, (B) habitat and (C) habitat plus edge (i.e. edge effects accounting for habitat effect) on each species occurrence from best Generalized Linear Models with binomial distribution and logit link function selected using Bayesian Information Criterion (BIC). Variables included in best models: D= distance to the urban boundary; HD= housing density (three levels: high housing density, low housing density, forested control); P.und= proportion of understory; MDS.1= first axis of the metric multidimensional scaling from habitat variables. W_x= best model BIC weight, shows the relative probability of the model being the best model of the candidate set. ΔBIC_{x-y}= Difference in BIC values between models "x" and "y". Letters show support of difference between models: W= weak; P= positive; S= strong; VS= very strong. Parenthesis ( ) indicate support in favour of "y" model. Models with highest support (i.e. lowest BIC) are shown in bold for each species.

Predictor type		Species occurrence							
		Brown antechinus	Bush rat	C. brushtail possum	Black wallaby	Long-nosed bandicoot	Red fox	Cat	Dog
Null	BIC_n	96.48	90.39	77.36	**59.89**	**41.36**	51.26	55.71	67.5
(A)									
Edge	Parameters	D^2	HD	D	D	D^2	D	HD+D+HDxD	**D**
	BIC_e	94.22	88.97	76.67	60.32	43.72	51.49	52.77	**60.62**
	W_e	0.51	0.42	0.38	0.53	0.51	0.5	0.29	0.52
	ΔBIC_{e-n}	-2.26 P	-1.42 W	-0.69 W	0.43 (W)	2.36 (P)	0.23 (W)	-2.94 P	-6.88 S
(B)									
Habitat	Parameters	**P.und**	**P.und**	**P.und**	MDS.1	P.und	**MDS.1**	**MDS.1**	P.und
	BIC_h	**88.14**	**76.59**	**64.13**	60.25	43.18	**47.73**	**42.79**	63.03
	W_h	0.57	0.69	0.66	0.57	0.41	0.71	0.5	0.44
	ΔBIC_{h-n}	-8.34 S	-13.8 VS	-13.23 VS	0.36 (W)	1.82 (W)	-3.53 P	-12.92 VS	-4.47 P
	ΔBIC_{h-e}	-6.08 S	-12.38 VS	-12.54 VS	-0.07 W	-0.54 W	-3.76 P	-9.98 S	2.41 (P)
(C)									
Habitat + edge	Parameters	P.und+D^2	P.und+D	P.und+D	MDS.1+D	P.und+D^2	MDS.1+D^2	MDS.1+D	P.und+D
	$BIC_{(h+e)}$	89.85	80.34	68.4	63.34	46.78	50.24	46.58	62.83
	$W_{(h+e)}$	0.57	0.42	0.44	0.48	0.43	0.55	0.35	0.53
	$\Delta BIC_{(h+e)-h}$	1.71 (W)	3.75 (P)	4.27 (P)	3.09 (P)	3.6 (P)	2.51 (P)	3.79 (P)	-0.2 W

Habitat effects on mammals

The first MDS axis represented a gradient from forests dominated by litter, projective foliage cover and woody debris (lower scores), to urban areas with high housing density dominated by impervious surfaces and bare ground (higher scores) (Figure 4, Supporting Information Table S4-S5). The second MDS axis described a gradient of declining grass cover and increasing impervious surfaces and bare ground (Figure 4, Supporting Information Table S4-S5).

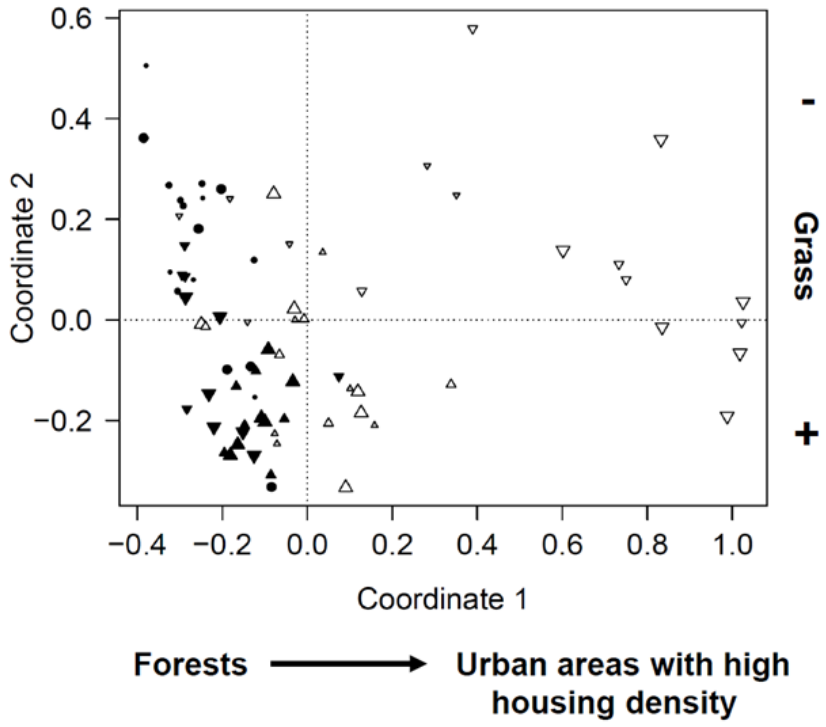


Figure 4. Metric multidimensional scaling of vegetation variables in camera stations. First axis shows a gradient from forests to urban areas with high housing density. Second axis shows a gradient of decline in grass cover. (▼) High housing density edge; (▲) Low housing density edge; (●) Forested control. Filling of symbols: Black= inside forest, Grey= boundary, White= inside urban area. Point size increases with distance from the boundary (as in Figure 1B).

Black wallaby and long-nosed bandicoot occurrence were best predicted by the null model. The proportion of understory cover at the camera stations was the best predictor of brown antechinus, bush rat, common brushtail possum and dog occurrence; whereas the first MDS axis (that represented a gradient from forests to urban areas with high housing density) was the best predictor of cat and red fox occurrence (Table 1B). The best habitat models provided positive, strong or very strong support when used to predict the occurrence of species compared to null models ($\Delta BIC>3$) and when compared to the best edge model ($\Delta BIC>3$), except for dog occurrence (Table 1B).

Edge effects after accounting for habitat effects on mammals

None of the models containing edge effects variables in addition to habitat variables was better than the habitat models alone. However, a model for the dog including the additive effect of understory cover and distance to the urban boundary had weak support ($\Delta BIC<2$) (Table 1C).

Best GLMMs predicting mammal occurrence

When variables only from the best edge models were fitted with GLMMs, which accounted for potential spatial autocorrelation between cameras within the same site, edge variables had a significant effect on the occurrence of the bush rat, cat and dog; and were marginally significant in models predicting the occurrence of brown antechinus and common brushtail possum (Table

2A). When variables from the best habitat models were fitted with GLMMs, the effect of habitat variables on mammal occurrence was significant for all species (Table 2B).

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Finally, when variables from the best habitat plus edge models were fitted with GLMMs, the significance of edge variables was removed, whereas the effect of habitat variables was significant for all species except the dog (Table 2C). That edge variables were no longer significant for the six species in the presence of habitat variables suggests some association or
360 collinearity between edge and habitat variables; and highlights that habitat variables accounted for all the variability associated with edge effects for most species.

Table 2. Variable estimates from Generalized Linear Mixed Models (GLMMs) with binomial distribution and logit link function of mammal occurrence from (A) edge, (B) habitat and (C) habitat plus edge best models. Variables included in best models: D= distance to the urban boundary; HD_{high}= high housing density, HD_{low}= low housing density; P.und= proportion of understory; MDS.1= first axis of the metric multidimensional scaling from habitat variables. When HD is included in models, controls were represented by the intercept. Bold denotes $P<0.1$.

		(A) Best edge model			(B) Best habitat model			(C) Best habitat + edge model		
Species	Variable	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Brown antechinus	Intercept	-1.26	0.33	**0.0001**	-2.38	0.57	**<0.0001**	-2.38	0.57	**<0.0001**
	D^2	0.0038	0.0023	**0.095**				0.0026	0.0022	0.23
	P.und				4.05	1.25	**0.001**	3.59	1.29	**0.005**
Bush rat	Intercept	-0.24	0.52	0.65	-3.16	0.70	**<0.0001**	-3.17	0.70	**<0.0001**
	HD_{high}	-2.46	0.94	**0.009**						
	HD_{low}	-0.65	0.68	0.34						
	D							0.030	0.040	0.45
	P.und				5.31	1.45	**0.0003**	4.99	1.50	**0.0009**
C. brushtail possum	Intercept	-1.30	0.33	**<0.0001**	0.34	0.59	0.57	0.31	0.61	0.61
	D	-0.16	0.094	**0.09**				-0.024	0.094	0.8
	P.und				-9.44	3.05	**0.002**	-9.03	3.37	**0.007**
Red fox	Intercept	-2.24	0.46	**<0.0001**	-2.94	0.60	**<0.0001**	-2.38	0.67	**0.0004**
	D	-0.24	0.17	0.16						
	D^2							-0.07	0.11	0.51
	MDS.1				2.69	0.99	**0.006**	2.51	1.06	**0.02**
Cat	Intercept	-2.8[a]	1.57[a]	**0.05**[a]	-2.9	0.59	**<0.0001**	-3.13	0.70	**<0.0001**
	HD_{high}	1.04[a]	1.71[a]	0.52[a]						
	HD_{low}	-0.63[a]	1.89[a]	0.73[a]						
	D	0.036[a]	0.078[a]	0.63[a]				0.061	0.072	0.40
	HD_{high} x D	-0.96[a]	0.37[a]	**0.001**[a]						
	HD_{low} x D	-0.036[a]	0.53[a]	0.96[a]						
	MDS.1				3.69	0.99	**0.0002**	4.16	1.22	**0.0006**

		(A) Best edge model			(B) Best habitat model			(C) Best habitat + edge model		
Species	Variable	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Dog	Intercept	-2.73	0.88	**0.002**	-0.77	0.99	0.44	-1.55	1.28	0.23
	D	-0.70	0.27	**0.009**				-0.51	0.32	0.11
	P.und				-9.40	4.06	**0.02**	-5.51	4.34	0.2

[a] Parameter estimates from Firth penalized logistic regression

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GLMMs revealed that the occurrence of the brown antechinus and bush rat increased with increased understory cover (Figure 5A-B). The occurrence of the brushtail possum decreased with increased understory cover (Figure 5C). Non-native species exhibited the highest occurrences in urban areas and the lowest occurrences in forests. The occurrence of the red fox and cat increased from forests to urban areas with high housing density (MDS.1 score) and the occurrence of the dog was highest in urban interiors and lowest in forest interior (Figure 5D-F).

Given our results, we performed supplementary analyses to investigate whether predators influenced the occurrence of prey (Wimp et al 2011). We evaluated the effect of exotic carnivores (i.e. a set of seven models, which were different combinations of the presence/absence of fox, cat and dog) on the occurrence of each native species (i.e. prey). We also explored the effect of predators after accounting for habitat effects by adding each predator model to the best habitat model of each species occurrence. None of the models including predators was better than the habitat model (Supporting Information Table S6).

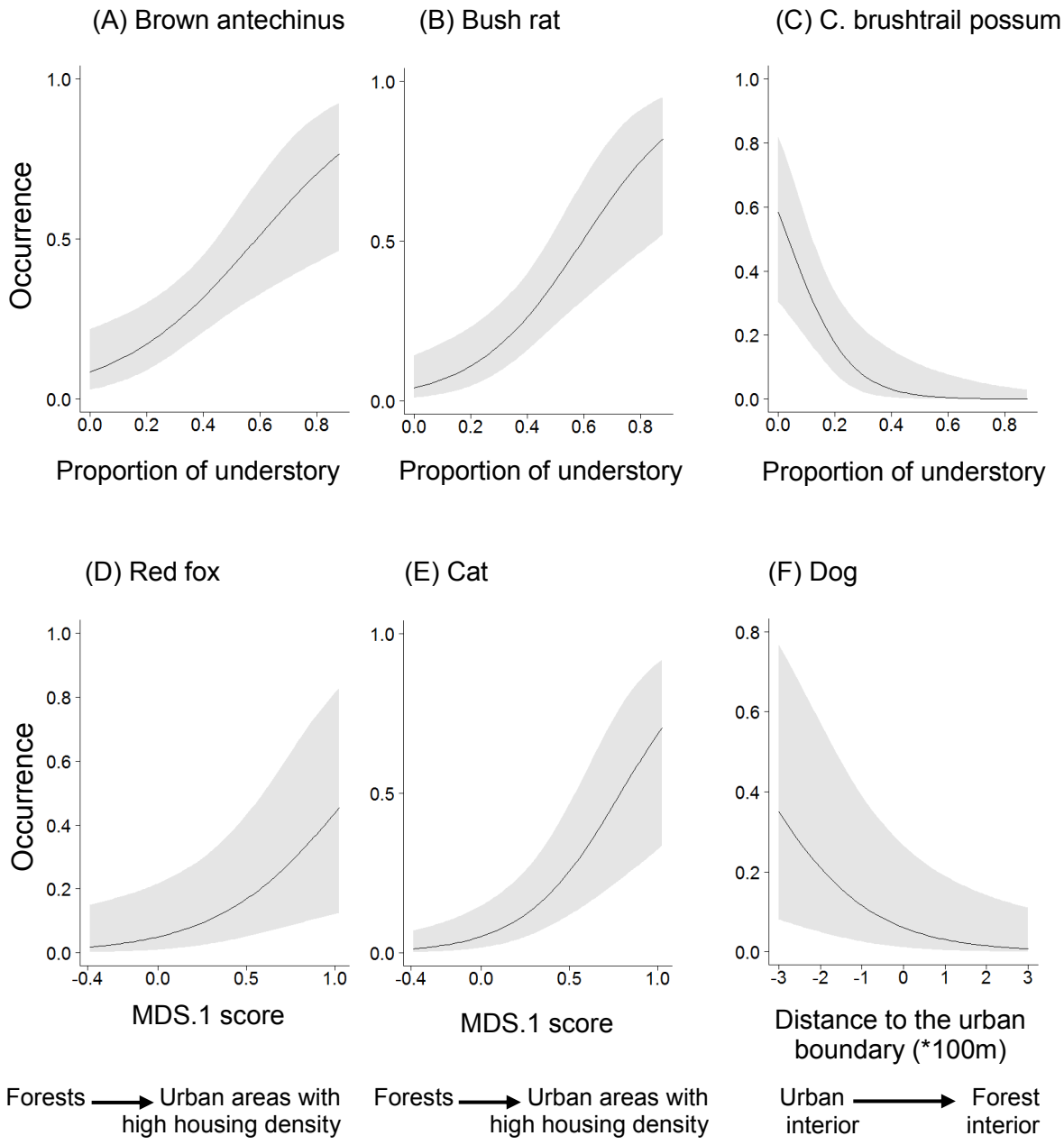

Figure 5. Estimated probability of occurrence in Generalized Linear Mixed Models (GLMMs) from models with highest support for (A) brown antechinus, (B) bush rat, (C) common brushtail possum, (D) red fox, (E) cat, and (F) dog. To optimize plot size for dog, distance to the boundary was shown up to 300 m into forests.

Discussion

Urbanization is a key process threatening biodiversity globally (McKinney 2006). Despite a rapid increase of urban-wildland interfaces (Stein et al 2012), ecological processes across urban-forest edges are poorly understood. For the first time, we tested whether the occurrence of mammals across urban-forest edges (including both sides of an urban boundary) and forest interiors was best predicted by edge variables or by local habitat structure. Edge variables, including housing density at the urban-forest edge and distance to the urban boundary, had weak effects on the occurrence of most mammals. In contrast, local habitat structure had stronger effects and accounted for most of the variation in the occurrence of five of eight mammals studied. Further, the effects of housing density and distance to the urban boundary mostly disappeared when considered together with habitat effects; indicating that local habitat structure explained most of the observed variation in the occurrence of mammals, which included edge effects. Our results suggested that conflicting responses by fauna to edge effects (Murcia 1995; Ries et al 2004; Battin and Sisk 2011) can result from weak edge effects on animals when relevant factors, such as local habitat attributes, are overlooked. We further discuss our results below, update conceptual models of edge effects, and provide strategies for ecologically sustainable urban development.

Strong local habitat effects on mammals

Habitat structure had a greater effect than edge variables on the occurrence of most mammals in our study (Tables 1-2). In particular, understory vegetation cover is an important variable for ground-dwelling mammals (Catling and Burt 1995; Van Dyck and Strahan 2008) and its cover

around camera stations was the best predictor for the occurrence of most native species. Brown antechinus and bush rat occurrence increased with increasing understory cover (Figure 5A-B), revealing that these forest species are sensitive to the reduction of understory. In contrast, the occurrence of the common brushtail possum decreased with increasing understory cover (Figure 5C), consistent with previous habitat descriptions for this marsupial, such as its tendency to avoid thick understory cover (Van Dyck and Strahan 2008). Although the distribution of this arboreal marsupial has been reduced across Australia, it is a common species in urban settlements (Villaseñor et al 2014), where it is able to find resources such as shelter and food (Eymann et al 2006). Only the black wallaby and long-nosed bandicoot were poorly predicted by habitat variables (Table 1), possibly as a result of their limited detection at our camera stations.

Non-native species occurrences were higher in urban areas than in forests (Figure 5D-F). According to the best habitat structure models that included MDS.1, the occurrence of the red fox and cat was lowest in forests and highest in residential areas with high housing density. Suburbs provide food, shelter and protection from lethal control (i.e. poisoning) for the red fox (Saunders et al 2010). Other authors have found that pet activity (i.e. cats and dogs) (Fandos et al 2012) and the occurrence of mesopredators (Červinka et al 2011) decline from the forest edge towards the forest interior. However, the spillover of carnivores from urban areas into adjacent forests appeared to be limited in our study area.

Weak edge effects on mammals

Previous research shows that the distribution of animals in mosaic landscapes is influenced by their response to habitat edges (Lidicker 1999; Ries et al 2004). However, there is considerable disagreement about the existence, intensity and type of response to edges (Murcia 1995; Ewers and Didham 2008; Battin and Sisk 2011). For instance, none of 16 ground-dwelling mammals in North America exhibited different abundance or activity at forest-farm edges when compared to forest interior (Heske 1995); whereas other studies have found small mammal abundance to be either highest (Šálek et al 2010) or lowest at edges (Mills 1995; Stevens and Husband 1998). Although distance to the urban boundary was more important than housing density at the edge in predicting the occurrence of most mammals in our study, these variables mostly had weak effects (Table 1). The findings of our study suggest that inconsistent results in the literature on edge effects can be a consequence of spurious relationships more likely to be found when key variables influencing species responses are overlooked (Watt and van den Berg 2002). For instance, species response to edges can be a result of bottom-up effects (e.g. food abundance; Mills 1995; Šálek et al 2010), as well as top-down effects (e.g. predator abundance; Wimp et al 2011). Further, confounding or interacting variables may change the magnitude, penetration or direction of edge effects (Ries et al 2004; Ewers and Didham 2006; Smith et al 2009). The discovery of strong effects of local habitat structure on most mammal occurrences (Tables 1-2) shows that variables other than edge types and distance to a boundary can underlie species occurrences across habitat edges.

Updating conceptual models for edge effects

Conceptual models of animal response across edges were developed at a patch level for simplicity, assuming homogeneity within patches on either side of the edge (Figure 6A). Two main explanatory variables are present in these models: edge type and distance to a boundary. Edge type focuses on dissimilarities between two adjacent patches in terms of different criteria: habitat quality, animal-habitat associations (Duelli et al 1990), qualitative resource distribution (Ries and Sisk 2004) or abundances of predator and prey (Lidicker 1999). To predict species responses across edges, a recent predictive model by Villaseñor et al (2014) integrated: (1) habitat quality and preference, (2) species response with the proximity to the adjacent habitat, and (3) modifying mechanisms which are associated with the species and environments involved (e.g. access, population dynamics). Although these edge effects models provide useful insights enabling better understanding of animal responses across edges, they ignore the effects of heterogeneity within patches.

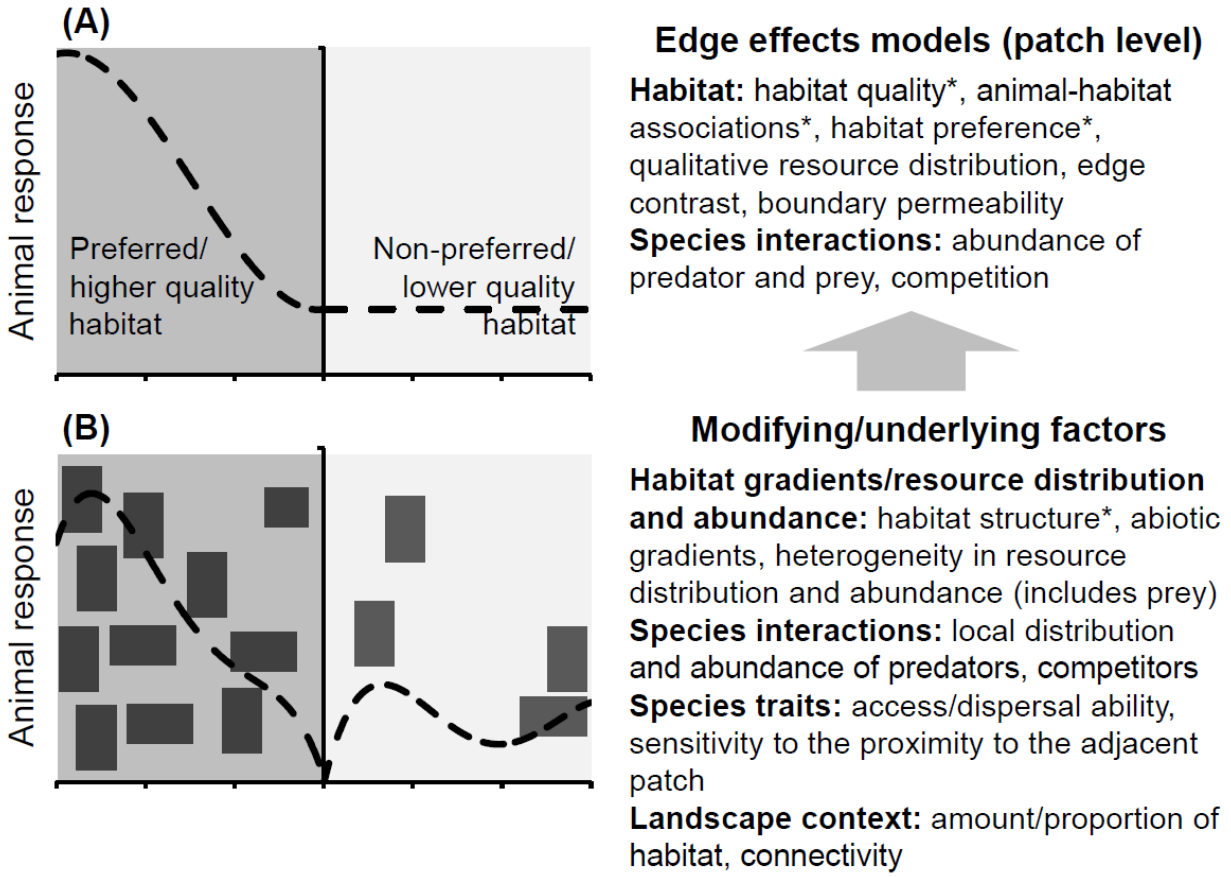

Figure 6. Representation of the mismatch in spatial scale (grain) between predictive variables in models of edge effects and modifying and underlying factors influencing a species response. (A) Graph shows a theoretical negative animal response (dashed line) with the proximity to the non-preferred or lower quality habitat (as described in Villaseñor et al (2014)). (B) Diagram shows the spatial heterogeneity of a covariate (rectangles; e.g. understorey cover) within patches. A negative animal response with the proximity to a boundary may be a result of a negative effect of the boundary on the covariate; but the covariate also can vary independently to the boundary, explaining additional variation. In the diagram, the covariate (e.g. understorey cover) is the main underlying factor influencing the animal response acorss the edge. (*) Variables used to build diagrams.

Patches and the surrounding matrix are not homogenous (Brearley et al 2011; Driscoll et al 2013) and this spatial heterogeneity influences populations (Ye et al 2013) (Figure 6B).

Therefore, variables at a higher spatial resolution (i.e. fine grain), such as local-scale attributes

within patches, can have an important effect on the response of species across edges. This influence of local-scale variables on species across edges can scale-up and influence populations at landscape and regional scales (Goddard et al 2010). Local-scale variables that are worth considering when predicting edge effects on animals may include: resource distribution and abundance (e.g. prey or host species abundance; Donovan et al 1997; Ries et al 2004), habitat gradients (e.g. habitat structure, abiotic gradients; Laurance 1991; Ries et al 2004; Harper et al 2005) and local-scale species interactions (e.g competitor and predator abundance; Donovan et al 1997; Villaseñor et al 2013). Further integration of local-scale variables along with target species traits in relation to the environment on either side of an edge (see Villaseñor et al 2014) and variables at a landscape scale (Donovan et al 1997; Šálek et al 2014) are needed when predicting animal responses across habitat edges and landscapes (Figure 6B).

Implications for management and urban planning

A better understanding of which landscape elements influence animal response across habitat edges is needed for effective conservation and urban planning. If edge variables have a greater influence on animals than local habitat structure, local management such as restoration will have a limited effect on animals, whereas the design and planning of urban areas will have major effects. We found edge effects on most mammals, but they were largely accounted for by local habitat structure (except for the dog). These results suggest that local-scale management of habitat can have an important effect on regulating mammal populations: both predators and prey. In particular, management strategies that increase understory cover are likely to have a positive

effect on native species and can be used to counteract the negative effects of edges on ground-dwelling mammals.

Given the key management implications of our work, a question that arises is: How can habitat structure be improved for native fauna in urbanizing landscapes? The retention of native vegetation at the planning stage; restoration strategies (e.g. tree and shrub planting, direct seeding, encouraging understory development) (Catling and Burt 1995); along with reducing the management of urban vegetation (e.g. mowing, pruning and felling) in public spaces will likely increase suitable habitat for wildlife (Do et al 2014). Unfortunately, in fire-prone regions, fire management of the vegetation (e.g. prescribed burning, clearing, slashing) to reduce fuel availability in an attempt to protect assets and residents (Radeloff et al 2005; Mell et al 2010) conflicts with the positive effects of increased vegetation cover on biodiversity (Driscoll et al 2010; Reed et al 2012; Le Roux et al 2014).

Because urban settlements are dominated by private lands with numerous households (Groffman et al 2014), management strategies must involve residents and property owners. For example, private gardens managed for wildlife can provide habitat for many species (Gaston et al 2005; Goddard et al 2010). Therefore, engaging people to provide habitat for wildlife will help mitigate the impacts of urbanization on biodiversity and meet conservation goals.

It is important to consider additional factors that can influence the outcomes of improved habitat structure on mammals. Although supplementary analyses confirmed that habitat had a stronger effect than ground-dwelling predators on prey; the red fox, cat and dog can nevertheless significantly affect native populations (Van Dyck and Strahan 2008; Paschoal et al 2012). Because these predators are common in urban settlements (Van Dyck and Strahan 2008), future research needs to evaluate their effect on the outcomes of improved habitat structure for native fauna in urban areas.

Despite habitat structure being the main factor influencing mammal occurrences, the confounded effects of edge (e.g. distance to an urban boundary) and habitat variables reveal that urban boundaries influence mammal distributions by modifying the habitat structure across urban-forest edges. We did not find strong edge effects on native mammals, but edge effects on core area species may extend long distances from urban development into adjacent habitats (Villaseñor et al 2014). Therefore, to reduce the effect of urban boundaries on adjacent habitats, it would be appropriate to decrease the amount of edges as part of urban development. Prioritizing clustered developments instead of dispersed developments might help to reduce the amount of natural habitat that is influenced by edge effects, helping to retain a larger amount of native vegetation at the landscape scale (Sushinsky et al 2013; Aronson et al 2014).

Our results suggest that improved habitat structure can ameliorate edge effects and urban impacts. Programs that aim to mitigate the impacts of urban development on wildlife must

consider: (1) improving habitat structure in public and private spaces; (2) engaging residents and property owners in education programs; and (3) reducing forest-urban edges when planning new urban areas. By considering these elements, residents, managers and land planners will help conserve biodiversity in an increasingly urbanizing world.

Approach and limitations

Our experimental design comprising mammal and habitat surveys along transects from forests to urban areas, allowed us to explore the effects of edge, habitat and habitat plus edge variables on mammal occurrence. We used GLMMs to estimate fixed effects while accounting for potential autocorrelation between cameras located within individual transects (i.e. sites). Vertically-oriented cameras aiming at a platform on the ground was an effective technique to record a wide variety of mammals without the loss of equipment (to avoid vandalism, cameras were secured with metal boxes, metal brackets and locks). Although camera trapping can be more cost-effective than live trapping for recording mammal occurrence (De Bondi et al 2010), cameras do not provide accurate estimations of species abundance when animals lack marks (Foster and Harmsen 2012) nor enable correct identification of morphologically similar species. Overall, vertically-oriented cameras are not only a cost-effective technique for monitoring several mammals at long temporal and large spatial scales (De Bondi et al 2010), but they also can be employed to collect empirical evidence and test hypotheses that inform ecologically sustainable urban development.

Conclusion

Our study is the first to test the variables that best predict mammal occurrence at both sides of an urban boundary. Our results demonstrate that local habitat structure (e.g. understory cover) had strong effects on mammal occurrences and outweighed the effects of edge variables (i.e. housing density at the edge and distance to an urban boundary). These findings have important implications for management, urban planning and landscape ecology theory. This is because they:

(1) provide support for a local-scale management of habitat and habitat retention as useful strategies to counteract the impacts of urban development on terrestrial fauna, and;

(2) highlight the need to consider heterogeneity within patches as a key variable influencing species responses in edge effects frameworks.

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