Clarifying habitat niche width using broad-scale, hierarchical occupancy models: A case study with a recovering mesocarnivore

Remington J. Moll[1,*], Kerry Kilshaw[2], Robert A. Montgomery[1,2], Leandro Abade[1,2], Ruairidh D. Campbell[2], Lauren A. Harrington[2], Joshua J.Millspaugh[3], J. D. S. Birks[4], David W. Macdonald[2]

[1]Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, United States of America

[2]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Tubney, Oxfordshire, United Kingdom

[3]School of Natural Resources, University of Missouri, Columbia, Missouri, United States of America

[4]Swift Ecology Ltd., West Malvern, Worcestershire, United Kingdom

[*] Corresponding author

E-mail: rjmoll@msu.edu

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Abstract

A species' habitat niche width informs its position on the generalist-specialist continuum, which is central to life history theory and crucial to conservation planning. However, assessments of niche width are often based on local-scale studies or qualitative descriptions rather than broad, quantitative assessments conducted in heterogeneous landscapes. Here, we show how broad-scale, hierarchical occupancy models can clarify a species' niche width and degree of habitat specialism by evaluating the woodland-specialist classification of the European pine marten (*Martes martes*). We deployed 526 camera-trap stations at 27 sites throughout a vast extent (~50,000km^2) in Scotland and modeled pine marten occupancy as a function of habitat characteristics using a hierarchical Bayesian analysis. Our model was flexible to trap-happiness due to baiting at camera-traps and accounted for spatial autocorrelation among and imperfect detection at camera-trap stations. We detected a positive association between pine marten occupancy probability and wooded habitats. However, pine marten occupancy probability was also high in numerous non-wooded habitats, including agricultural land, heather and heather grassland, semi-natural grassland, and areas near anthropogenic structures. Our study is the first to record high pine marten occupancy in open habitats at broad spatial scales and thereby corroborates recent smaller-scale indications that pine martens are more of a habitat generalist than previously thought. Our results guide ongoing conservation efforts by identifying that pine martens are not strict woodland-specialists, but rather inhabit a mosaic of habitat types in the landscape. More broadly, our case study exemplifies how coupling hierarchical occupancy models with large-scale experimental designs can clarify a species' niche width and associated position on the generalist-specialist continuum.

Keywords

habitat niche, Bayesian analysis, hierarchical occupancy models, Martes martes, specialist-generalist, trap-happiness

Introduction

Correctly positioning species along the generalist-specialist continuum is central to life history theory and has important implications for conservation planning. For instance, genetic isolation (Futuyma & Moreno, 1988), effective population size (Zayed *et al.*, 2005), ability to serve as a biological control of invasive species (Landis, Wratten & Gurr, 2000), contribution to ecosystem stability (Tylianakis *et al.*, 2010), response to agricultural practice (Filippi-Codaccioni *et al.*, 2010), and sensitivity to habitat loss, disturbance, and fragmentation (Devictor, Julliard & Jiguet, 2008) all depend on the specialist versus generalist life history traits of the organisms of interest.

Specialist/generalist classification is rooted in habitat niche width theory, which purports that a species' fitness is a function of its ability to exploit resources across heterogeneous environments (Clavel, Julliard & Devictor, 2011). Specialists have a narrow habitat niche and require specific characteristics, whereas generalists have a wide niche and thrive in a variety of settings (Devictor *et al.*, 2008; Dennis *et al.*, 2011). Despite the conservation implications of generalist/specialist life history traits and the well-established concept of niche width in ecological theory, generalist/specialist classifications have often relied on qualitative descriptions and/or local-scale studies rather than quantitative assessments conducted over broad scales, particularly for wide-ranging organisms (Futuyma & Moreno, 1988; Pardini *et al.*, 2009;

Devictor *et al.*, 2010). Moreover, species of lesser conservation concern might be especially prone to misclassification due to a lack of research effort (e.g., see Ruiz-Gutiérrez, Zipkin & Dhondt, 2010). Therefore, while broad-scale, quantitatively rigorous assessments are required to accurately define a species' habitat niche width and associated degree of specialism (Clavel *et al.*, 2011), such assessments are severely lacking for wide-ranging organisms (e.g., terrestrial carnivores) that are not under immediate threat of extinction (cf. Futuyma & Moreno, 1988). However, recent advances in technology (e.g., camera-traps; Burton *et al.*, 2015) and species distribution modeling (e.g., hierarchical occupancy models; Royle & Dorazio, 2008) afford a means to address this problem.

Here we present a case study that demonstrates how a broad-scale, hierarchical occupancy model can clarify a species' habitat niche width and position on the generalist-specialist continuum. We use an extensive camera-trapping network to model the occurrence of a recovering mesocarnivore, the European pine marten (*Martes martes*), across a vast (50,000km^2) landscape in Scotland. Martens are a legally protected priority species in the United Kingdom Biodiversity Action Plan and remain rare in Scotland despite recent trends towards recovery (Birks, 2002; Baines *et al.*, 2013). Pine martens have traditionally been regarded as woodland specialists (Brainerd, 1990; Storch, Lindstrom & de Jounge, 1990; Balharry, 1993), a trait that, if accurate, has important implications for conservation and management. However, research in the 1990s posited that the specialist classification of pine martens was too strict (e.g., Clevenger, 1994) and recent smaller-scale studies suggest that pine martens are more of a habitat generalist than previously thought (Pereboom *et al.*, 2008; Balestrieri *et al.*, 2010; Caryl, Quine & Park, 2012a). We present a large-scale, quantitatively rigorous test of this hypothesis. We discuss the

utility of broad-scale studies for clarifying a species' position along the generalist-specialist continuum and consider the implications of our results for pine marten conservation.

Materials and methods

Study area

We conducted our study in the Scottish Highlands (area ~50,000km^2). The spatial extent of our study area translates to a wide variety of habitat types and climactic conditions. Generally, average annual temperatures and rainfall increase moving from east to west across the study region, and snowfall is common in upland and mountainous regions (e.g., the Grampian mountains) in the north and east (MET, 2012). Approximately 20% of the Highlands are woodland and 44% consist of a mosaic of heather moorland/peatland. Woodland habitat primarily consists of conifer forest plantations with smaller proportions of native conifer and broadleaf woodlands. The eastern lowlands are primarily woodlands and agriculture. Mean human population density in this region is <10 people/km^2 (SCROL, 2011).

Experimental design

From November 2010-July 2013 we deployed 526 camera-trap stations at 27 sites in the Scottish Highlands, which were generally chosen due to a historic or recent record of Scottish wildcats (*Felis silvestris silvestris*) for a concomitant study on that species. This sampling design resulted in sites that included the full range of habitat types available in the Highlands, with only high elevations (i.e., >800m) and the most highly urbanized or agriculturally developed areas (i.e., >86% agriculture) being avoided (Supporting Information Fig. S1 and Table S1). At each site, we deployed ~20 camera-trap stations ($\bar{x}$ = 19.5, sd = 3.1), each comprised of two camera-

traps with overlapping view sheds, in an approximate 4 x 5 km grid. We affixed camera-traps to trees or posts 20-50cm above the ground. We baited traps with dead pheasant (*Phasianus colchicus*), red-legged partridge (*Alectoris rufa*), and a scent lure (valerian tincture). We replaced bait every 10-14 days. We sampled each site once and camera-trap stations were active between 60 and 80 days at a given site.

Habitat covariates and modeling framework

Preliminary data exploration indicated a lack of seasonal or yearly variation in either occupancy or detection rates over the study period. Therefore, we modeled pine marten occupancy as a function of habitat covariates. We drew upon the literature and our own experience to identify relevant habitat covariates and their expected relationship to pine marten occupancy (Table 1).

Pine martens in Scotland have been positively associated with woodland habitat, including natural deciduous woodland (Balharry, 1993; Halliwell, 1997; Caryl *et al.*, 2012a), natural coniferous woodland (i.e., Scots pine *Pinus sylvestris*; Caryl *et al.*, 2012; Baines *et al.*, 2013), and commercial coniferous plantations typically consisting of Scots pine, larch *Larix* spp. and/or spruce *Picea* spp (Balharry, 1993; Bright, 1997; Baines *et al.*, 2013; see Caryl *et al.*, 2012a for exception). Pine martens tend to avoid agricultural land (Balharry, 1993; Halliwell, 1997; Pereboom *et al.*, 2008; Caryl *et al.*, 2012a; Lombardini *et al.*, 2015), although recent studies in Italy suggest they might be colonizing agricultural areas (Balestrieri *et al.*, 2010, 2011; cf. Manzo *et al.*, 2012). Early work in Scotland suggested that martens broadly avoided all non-wooded habitat due predation risk from red foxes (*Vulpes vulpes*) and golden eagles (*Aquila chrysaetos*; Balharry, 1993; Halliwell, 1997). However, recent work suggests martens tolerate,

and perhaps benefit from, moderate fragmentation due to increased access to prey in edge habitats (Caryl *et al.*, 2012a; Virgós *et al.*, 2012). Finally, pine martens tend to avoid urbanized areas (Lombardini *et al.*, 2015), but might use anthropogenic structure (e.g., farm buildings) for den sites when natural vegetation structure is scarce (Birks, Messenger & Halliwell, 2005).

We modeled pine marten occupancy using covariates derived from land cover types representing the habitats described above (Table 1). We used broad habitat classifications of the 2007 United Kingdom Land Cover Map (under license LCM 2012-357vs2) to depict land cover type as proportions of habitat in 0.25km^2 raster cells in ArcMap 10.2.1 throughout Scotland. Our two wooded cover types (deciduous/mixed woodland and coniferous forest; Table 1) included mature woodland, regenerating woodland, scrub, and felled stands. At finer scales (e.g., home range), pine marten resource selection and/or population density might vary among these sub-habitats (Caryl *et al.*, 2012a). However, there is evidence that all provide suitable habitat for pine martens and thus broad-scale pine marten occurrence is likely similar within our broader categories (Balharry, 1993; Bright, 1997). We used the United Kingdom Ordnance Survey to develop a cost-distance raster for distance to the nearest anthropogenic structure, including urban and rural settlements as well as farm buildings, retail parks, and urban parkland. To make this raster we first created a cost raster depicting *terra firma* in Scotland, which ensured that distance would be calculated around, rather than across, natural barriers, including lochs, coastal bays, and inlets. We then used the *cost distance tool* in ArcMap to calculate the cost-distance from every cell in the study area to the nearest anthropogenic structure. We created the edge covariate by creating a binary layer representing closed (coniferous forest and mixed/deciduous woodland) and open (semi-natural grassland, heather, and gorse habitat characterized by *Ulex europaeus*) habitats. We intersected camera-trap station locations with these rasters to develop spatially-

explicit measures of covariates at each station. Variance inflation factors of the covariates suggested a lack of multicollinearity (cutoff of 3.0; Zuur, Ieno & Elphick, 2010). We standardized predictor variables to have a mean of 0 and a standard deviation of 1 (Kéry, 2010).

We modeled pine marten occupancy in a hierarchical framework. We binned detection/non-detection data for each station into one-week survey replicates (8-12 replicates/site). Given pine martens' relatively stable, non-overlapping territories and high home range fidelity (Bright, 1997), we assumed a closed population over the sampling period at each site (i.e., ~10 weeks; Mackenzie *et al.*, 2002). We modeled true occupancy at camera station *i* as a latent variable, z_i, that is Bernoulli distributed with a probability ψ_i such that $z = 1$ if station *i* is occupied and is zero otherwise. Given that pine marten home ranges could encompass multiple camera stations (Caryl *et al.*, 2012a), we built our model to accommodate spatial autocorrelation by modeling the intercept as a random effect at the site level (Rhodes *et al.*, 2009). Spline correlograms indicated this procedure reduced autocorrelation in model residuals to acceptable levels, thus meeting our model's independence assumptions (Supporting Information Fig. S2). Our occupancy model had the final form:

$$\text{logit}(\psi_i) = \alpha_{site} + \alpha_1*\text{agriculture}_i + \alpha_2*\text{conifer}_i + \alpha_3*\text{edge}_i + \alpha_4*\text{sgrassland}_i + \alpha_5*\text{heather}_i + \alpha_6*\text{structure}_i + \alpha_7*\text{woodland}_i, \quad (1)$$

where ψ_i is the occupancy probability at the *i*th camera station, α_{site} is a normally distributed random variable whose mean μ and variance σ^2 are estimated, site-level hyperparameters, and habitat covariates are values extracted from 0.25km^2 raster cells (Table 1; model code in Supporting Information Appendix S1).

Given imperfect detection at a given station, we modeled detection probability given a species' true occupancy, z_i (Mackenzie *et al.*, 2002). Initial data exploration suggested a lack of effect of habitat covariates on the detection process. Thus, we designed our model to be flexible to temporal patterns in pine marten detection due to baiting (ephemeral trap-happiness; Kéry & Schaub, 2012). Accordingly, detection for the first survey was:

$$y_{i,1} | z_i \sim \text{Bernoulli}(p_{i,j} * z_i) \quad (2)$$

and

$$y_{i,j>1} | z_i \sim \text{Bernoulli}([(1 - y_{i,j-1}) * p + y_{i,j-1} * q] * z_i) \quad (3)$$

for all subsequent replicates, where $y_{i,j}$ is detection/non-detection data for station i during replicate j, z_i is true occupancy at station i, and p and q are detection probabilities given non-detection and detection in the previous replicate, respectively.

Model analysis and selection

We analyzed our model in a Bayesian framework using Markov chain Monte Carlo (MCMC) simulations run in R (R Development Core Team, 2011) and JAGS (Plummer, 2003) via the package R2jags (Su & Yajima, 2012). We evaluated the level of support for habitat covariates using a Bayesian inclusion parameter, w_c (Kuo & Mallick, 1998). Inclusion parameters were Bernoulli distributed with a non-informative prior probability of 0.5. The posterior of w_c represents the probability that covariate C is included in the best model in the set of 2^C candidate models (Royle & Dorazio, 2008; Burton *et al.*, 2012). We calculated model-averaged coefficients over the full model from MCMC posterior histories (Royle & Dorazio, 2008, pg. 72-73). We used diffuse priors and ran 3 chains of 20,000 iterations each after a burn-

in of 5,000 and thinned the posterior chains by 10. Parameters converged successfully (R-hat values <1.1; Gelman & Hill, 2007). For model validation, we used the posterior distribution of *z* values at each station and model predictions to calculate the area under the curve (AUC) using the package pROC (Robin *et al.*, 2011; Zipkin, Grant & Fagan, 2012). Finally, we produced a predictive occupancy map by multiplying model coefficients (Eq. 1) with the covariate rasters across the full extent of Scotland.

Results

We recorded a 5,875 camera-trap weeks (41,125 camera-trap days). These raw data indicated that 292 of the 526 stations (55.5%) and all 27 sites were occupied by pine martens. We also detected pine martens at 12 out of 28 (42.9%) camera-trap stations in 0.25km^2 cells containing >50% agricultural habitat and 20 out of 89 (22.5%) camera-trap stations in 0.25km^2 cells lacking wooded or forested habitat.

Pine martens exhibited ephemeral trap-happiness ($q > p$; Table 2). Accounting for imperfect detection, our model estimated ~337 out of 526 stations (64.0%) were occupied (95% credible interval (CI): 322, 355; Table 2). Occupancy probability was near 1.0 in areas with high proportions of coniferous forest and/or deciduous/mixed woodland and near 0 in areas with little woodland or forested habitat and far from anthropogenic structure (Fig. 1). The mean AUC derived from the posterior distribution of *z* values (0.70) indicated acceptable model fit (Manel, Williams & Ormerod, 2001).

Respective inclusion probabilities for proportion coniferous forest and deciduous/mixed woodland in a given 0.25km^2 cell were 0.98 and 1.0, and both covariates exhibited a strong positive relationship with occupancy (Table 2, Fig. 2a,b).

Inclusion probabilities for all other covariates were low (i.e., ≤0.12; Table 2) and all 95% CIs for these covariates overlapped zero (Table 2). Distance to anthropogenic structure exhibited a weak negative relationship with pine marten occupancy probability (Fig. 2c). Proportion agriculture, proportion semi-natural grassland, proportion heather, and amount of edge in a 0.25km^2 cell all exhibited weak positive associations with pine marten occupancy probability (Fig. 2d-g).

Discussion

Here, we used a case study to exhibit how broad-scale, hierarchical occupancy models can clarify a species' habitat niche width and position on the generalist-specialist continuum. Specifically, the scale of our assessment captured heterogeneity in a variety of environmental factors, which is crucial for accurately describing niche width (Devictor *et al.*, 2010). In addition, the form of our occupancy model accounted for imperfect detection at camera-stations and spatial autocorrelation among them, both of which could bias species-habitat associations if unconsidered (Kéry & Schaub, 2012). Given the dual ubiquity of camera-trapping methods (Burton *et al.*, 2015) and occupancy modeling (Royle & Dorazio, 2008), the approach demonstrated here could be broadly applied in a variety of settings to update or refine species' habitat niche width and position on the generalist-specialist continuum.

To our knowledge, our case study is the first to explicitly quantify high pine marten occurrence in open habitats at broad scales. As such, it corroborates recent evidence from finer-scale assessments which illustrated that the habitat niche of pine martens is wider than previously thought (Pereboom *et al.*, 2008; Balestrieri *et al.*, 2010; Caryl *et al.*, 2012a). Others have found a positive relationship between pine martens and ungrazed grasslands (Caryl *et al.*, 2012a) and a

negative association with agricultural lands (Balharry, 1993; Pereboom *et al.*, 2008; Caryl *et al.*, 2012a; Manzo *et al.*, 2012; Lombardini *et al.*, 2015). We found little evidence for such relationships at a broad scale. Given that pine marten home ranges can encompass a variety of habitat types, it is possible that these habitats are preferred or avoided on a finer-scale but do not influence overall pine marten occupancy in Scotland. We conclude that while pine martens are positively associated with woodland/forested habitat, they also occupy a variety of environments, including areas near anthropogenic structure, open habitats such as heather and semi-natural grasslands, and areas containing sizable amounts (i.e., 25-75%) of agricultural land (Fig. 1, Fig. 2). In context with other recent studies, our results suggest that at broad scales pine martens are perhaps best classified as moderate habitat generalists that require a relatively modest baseline level of structurally complex, wooded habitat (Balestrieri *et al.*, 2010; Mergey, Helder & Roeder, 2011; Caryl *et al.*, 2012a; Larroque *et al.*, 2016). Other aspects of pine marten ecology, including their behavioral plasticity in relation to mobility, home range size, and diet (Bright, 1997; Lynch & McCann, 2007; Balestrieri *et al.*, 2011; Caryl *et al.*, 2012a, 2012b; Virgós *et al.*, 2012), support a generalist-leaning classification, as do studies showing pine martens maintain genetic connectivity in fragmented landscapes (Mergey *et al.*, 2011; Larroque *et al.*, 2016)

Our case study supports the notion that the degree of habitat specialization observed for a given species can change with scale and context (Devictor *et al.*, 2010). For example, Balharry (1993) found pine martens tended to prefer woodland and commercial forest plantations and avoid open areas, but the strength of preference varied by study site and spatial scale (i.e., study site vs. home range). Similarly, Caryl *et al.* (2012a) found pine martens in Scotland selected structurally complex wooded habitats and grasslands while avoiding agriculture and closed-canopy coniferous stands, but these preferences disappeared within home ranges. In addition,

Clevenger (1994) found that pine martens lacked any habitat preference on a Mediterranean island, a result that was attributed to the local absence of predators. More broadly, the majority of studies evaluating habitat preference of pine martens have been conducted in localized, heavily wooded regions of Fennoscandia (e.g., Brainerd, 1990; Storch *et al.*, 1990; Brainerd *et al.*, 1995; cf. Caryl *et al.*, 2012a), have focused on particular seasons (e.g., snow tracking in winter; Storch *et al.*, 1990), and/or have relied on modest sample sizes (e.g., Balharry, 1993; Halliwell, 1997; Pereboom *et al.*, 2008; and Caryl *et al.*, 2012a radiotracked a mean of 8.3 pine martens (sd = 3.4) per study site). While the conclusions reached by such studies are likely relevant to their particular contexts and scales, our broad-scale approach contributes to a more generalized classification of pine martens (Devictor *et al.*, 2010), with two important caveats. First, our study sites had a moderate mean proportion of woodland (0.43) and the broader area had low densities of humans and anthropogenic structure. Thus, additional work is required to evaluate our results to more populous or heavily deforested regions. Second, our study area lacked one of the pine marten's competitors, the stone marten (*Martes foina*). Due to habitat niche segregation, pine martens inhabiting areas where these species are sympatric might more strongly prefer woodlands than in our study area (Wereszczuk & Zalewski, 2015).

Our approach highlights the importance of accounting for imperfect detection in occupancy models. Ignoring imperfect detection in our study would have resulted in underestimating occupancy by 8.5% (Table 2). Such underestimation could bias generalist-specialist species classifications (Kéry & Schaub, 2012) and might cause conservation concern where it is unwarranted, especially for elusive species (Mackenzie *et al.*, 2002). Moreover, our research found an ephemeral trap-happy response in pine martens, likely due to the use of bait (Kéry & Schaub, 2012). Although recent work on Pacific martens (*Martes caurina*) suggested

their winter habitat associations were biased by baiting (Moriarty *et al.*, 2015), we found no evidence of such bias in our study in *post hoc* analysis (i.e., habitat covariates had no relationship with seasonal detection rates, nor with degree of trap-happiness). This is likely because we baited less frequently (once every 10-14 days vs. once every 4-5 days) and placed our camera stations much farther apart (~1000m vs. 50m) than Moriarty *et al.* (2015).

Agencies interested in conservation actions (e.g., reintroducing pine martens into Wales; MacPherson *et al.*, 2014) might use modeling approaches similar to those described here to prioritize efforts for species' recovery. For instance, our predictions suggest pine martens will occupy habitat near human development or agricultural land, provided the broader area contains a baseline level of wooded habitat (i.e., 0.25km^2 patches with a minimum of 20-40% wooded cover; cf. Larroque *et al.*, 2016; Fig. 2a,b). Our predictive occupancy map comes with the caveat that our survey sites were confined to the Scottish Highlands. However, extrapolated occupancy probabilities for southern Scotland and surrounding islands (Fig. 1), where pine martens are currently scarce, depict areas of habitat that could be targeted for reintroduction or reinforcement efforts, if additional studies validate the suitability of these locations.

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References

Baines, D., Aebischer, N., Macleod, A. & Woods, J. (2013). Pine marten *Martes martes* and red fox *Vulpes vulpes* sign indices in Scottish forests: population change and reliability of field identification of scats. *Wildlife Biol.* **19**, 490–495.

Balestrieri, A., Remonti, L., Ruiz-González, A., Gómez-Moliner, B.J., Vergara, M. & Prigioni, C. (2010). Range expansion of the pine marten (*Martes martes*) in an agricultural landscape matrix (NW Italy). *Mamm. Biol.* **75**, 412–419.

Balestrieri, A., Remonti, L., Ruiz-González, A., Vergara, M., Capelli, E., Gómez-Moliner, B.J. & Prigioni, C. (2011). Food habits of genetically identified pine marten (*Martes martes*) expanding in agricultural lowlands (NW Italy). *Acta Theriol.* **56**, 199–207.

Balharry, D. (1993). *Factors affecting the distribution and population density of pine martens (Martes martes L.) in Scotland*. University of Abderdeen.

Birks, J.D.S. (2002). *The Pine Marten*. Southampton, England: The Mammal Society.

Birks, J.D.S., Messenger, J.E. & Halliwell, E.C. (2005). Diversity of den sites used by pine martens *Martes martes*: A response to the scarcity of arboreal cavities? *Mamm. Rev.* **35**, 313–320.

Brainerd, S.M. (1990). The pine marten and forest fragmentation: a review and general hypothesis. In *Transactions of the Nineteenth International Conference of Game Biologists*: 421–434.

Brainerd, S.M., Helldin, J.O., Lindstrom, E.R., Rolstad, E., Rolstad, J. & Storch, I. (1995). Pine marten (*Martes martes*) selection of resting and denning sites in Scandinavian managed forests. *Ann. Zool. Fennici* **32**, 151–157.

Bright, P.W. (1997). *Species recovery programme for the pine marten in England: 1995-1996*.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E. & Boutin, S. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* **52**, 675–685.

Burton, A.C., Sam, M.K., Balangtaa, C. & Brashares, J.S. (2012). Hierarchical multi-species modeling of carnivore responses to hunting, habitat and prey in a West African protected area. *PLoS One* **7**, e38007.

Caryl, F.M., Quine, C.P. & Park, K.J. (2012a). Martens in the matrix: the importance of nonforested habitats for forest carnivores in fragmented landscapes. *J. Mammal.* **93**, 464–474.

Caryl, F.M., Raynor, R., Quine, C.P. & Park, K.J. (2012b). The seasonal diet of British pine marten determined from genetically identified scats. *J. Zool.* **288**, 252–259.

Clavel, J., Julliard, R. & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* **9**, 222–228.

Clevenger, A.P. (1994). Habitat characteristics of Eurasian pine martens *Martes martes* in an insular Mediterranean environment. *Ecography.* **17**, 257–263.

Dennis, R.L.H., Dapporto, L., Fattorini, S. & Cook, L.M. (2011). The generalism-specialism debate: the role of generalists in the life and death of species. *Biol. J. Linn. Soc.* **104**, 725–737.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. & Mouquet, N. (2010). Defining and measuring ecological specialization. *J. Appl. Ecol.* **47**, 15–25.

Devictor, V., Julliard, R. & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* **117**, 507–514.

Filippi-Codaccioni, O., Devictor, V., Bas, Y., Clobert, J. & Julliard, R. (2010). Specialist response to proportion of arable land and pesticide input in agricultural landscapes. *Biol. Conserv.* **143**, 883–890.

Futuyma, D.J. & Moreno, G. (1988). The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.* **19**, 207–233.

Gelman, A. & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models.*

New York, New York: Cambridge University Press.

Halliwell, E.C. (1997). *The ecology of red squirrels in Scotland in relation to pine marten predation*. University of Aberdeen.

Kéry, M. (2010). *Introduction to WinBUGS for ecologists: A Bayesian approach to regression, ANOVA, mixed models and related analyses*. San Diego, California: Academic Press.

Kéry, M. & Schaub, M. (2012). *Bayesian population analysis using WinBUGS: a hierarchical perspective*. San Diego, California: Academic Press.

Kuo, L. & Mallick, B. (1998). Variable selection for regression models. *Sankhya Ser.B* **60**, 65–81.

Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* **45**, 175–201.

Larroque, J., Ruette, S., Vandel, J.-M. & Devillard, S. (2016). Divergent landscape effects on genetic differentiation in two populations of the European pine marten (*Martes martes*). *Landsc. Ecol.* **31**, 517–531.

Lombardini, M., Cinerari, C.E., Murru, M., Vidus Rosin, A., Mazzoleni, L. & Meriggi, A. (2015). Habitat requirements of Eurasian pine marten *Martes martes* in a Mediterranean environment. *Mammal Res.*

Lynch, A.B. & McCann, Y. (2007). The diet of the pine marten (*Martes martes*) in Killarney National Park. In *Biology and Environment: Proceedings of the Royal Irish Academy*: 67–76.

Mackenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.

MacPherson, J., Croose, E., Bavin, D., O'Mahony, D., Somper, J.P. & Buttriss, N. (2014). *Feasibility assessment for reinforcing pine marten numbers in England and Wales*. Ledbury, Herefordshire, England.

Manel, S., Williams, H.C. & Ormerod, S.J. (2001). Evaluating presence absence models in ecology; the need to count for prevalence. *J. Appied Ecol.* **38**, 921–931.

Manzo, E., Bartolommei, P., Rowcliffe, J.M. & Cozzolino, R. (2012). Estimation of population density of European pine marten in central Italy using camera trapping. *Acta Theriol. (Warsz).* **57**, 165–172.

Mergey, M., Helder, R. & Roeder, J.-J. (2011). Effect of forest fragmentation on space-use patterns in the European pine marten (*Martes martes*). *J. Mammal.* **92**, 328–335.

MET. (2012). MET Office climate data [WWW Document]. URL www.metoffice.gov.uk/climate/uk/ns/

Moriarty, K.M., Epps, C.W., Betts, M.G., Hance, D.J., Bailey, J.D. & Zielinski, W.J. (2015). Experimental evidence that simplified forest structure interacts with snow cover to influence functional connectivity for Pacific martens. *Landsc. Ecol.* **30**, 1869–1881.

Pardini, R., Faria, D., Accacio, G.M., Laps, R.R., Mariano-Neto, E., Paciencia, M.L.B., Dixo, M. & Baumgarten, J. (2009). The challenge of maintaining Atlantic forest biodiversity: A

multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. *Biol. Conserv.* **142**, 1178–1190.

Pereboom, V., Mergey, M., Villerette, N., Helder, R., Gerard, J.-F. & Lodé, T. (2008). Movement patterns, habitat selection, and corridor use of a typical woodland-dweller species, the European pine marten (*Martes martes*), in fragmented landscape. *Can. J. Zool.* **86**, 983–991.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*: 124:1–8.

R Development Core Team, R. (2011). R: A language and environment for statistical computing.

Rhodes, J.R., McAlpine, C.A., Zuur, A.F., Smith, G.M. & Ieno, E.N. (2009). GLMM applied on the spatial distribution of koalas in a fragmented landscape. In *Mixed effects models and extensions in ecology with R*: 469–492. New York, New York: Springer.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.C. & Müller, M. (2011). pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics* **12**, 77.

Royle, J.A. & Dorazio, R.M. (2008). *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities.* Oxford, UK: Elsevier Academic Press.

Ruiz-Gutiérrez, V., Zipkin, E.F. & Dhondt, A.A. (2010). Occupancy dynamics in a tropical bird

community: Unexpectedly high forest use by birds classified as non-forest species. *J. Appl. Ecol.* **47**, 621–630.

SCROL. (2011). Scotland's Census Results Online [WWW Document]. URL www.scrol.gov.uk

Storch, I., Lindstrom, E. & de Jounge, J. (1990). Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriol.* **35**, 311–320.

Su, Y.S. & Yajima, M. (2012). R2jags: a package for running jags from R.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010). Conservation of species interaction networks. *Biol. Conserv.* **143**, 2270–2279.

Virgós, E., Zalewski, A., Rosalino, L.M. & Mergey, M. (2012). Habitat ecology of Martes species in Europe. In *Biology and Conservation of Martens, Sables, and Fishers: A New Synthesis*. Aubry, K.B., Zielinski, W.J. & Raphael, M.G. (Eds). Ithaca, NY, USA: Comstock Pub. Associates.

Wereszczuk, A. & Zalewski, A. (2015). Spatial niche segregation of sympatric stone marten and pine marten - Avoidance of competition or selection of optimal habitat? *PLoS One* **10**, e0139852.

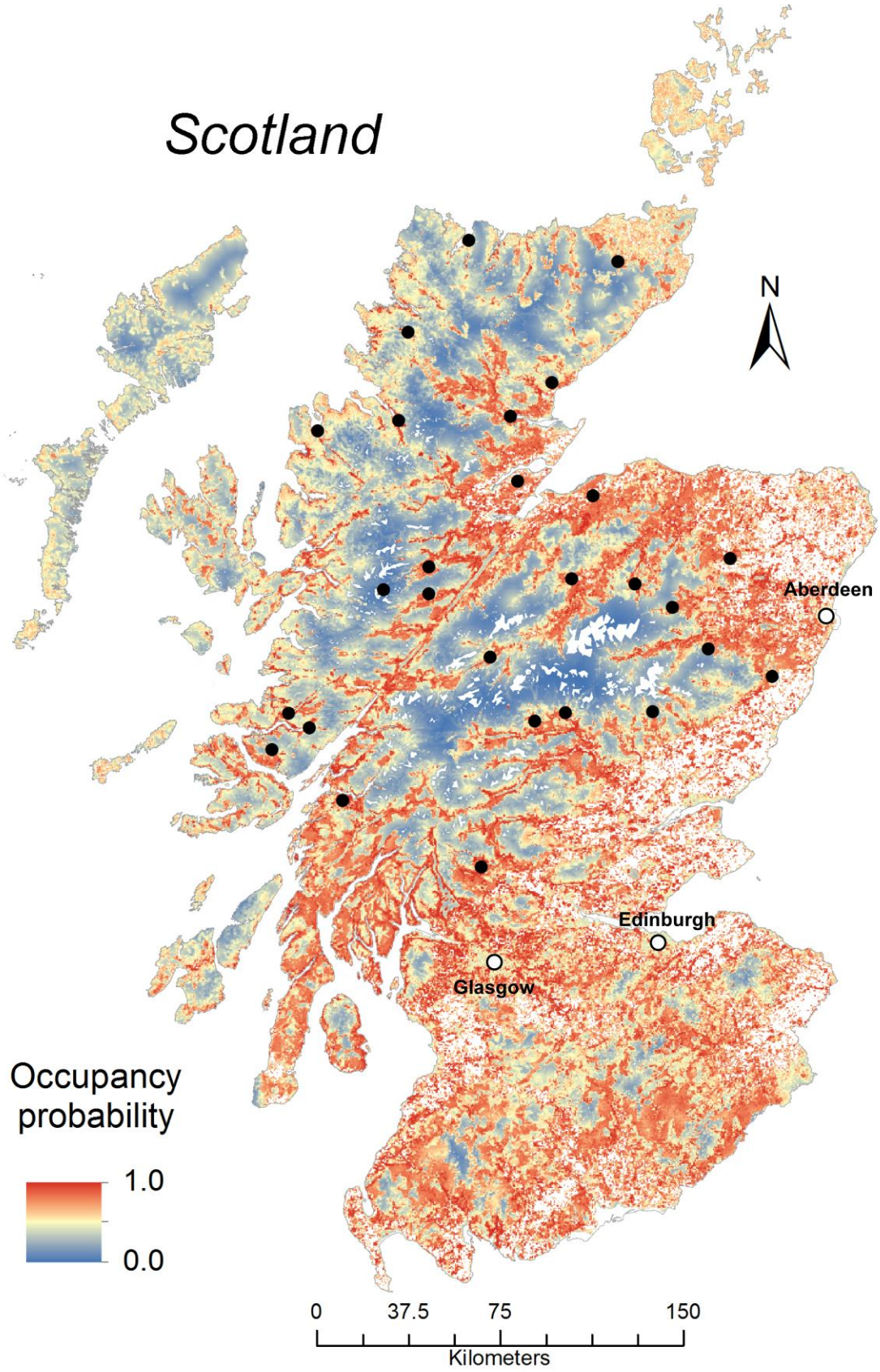
Zayed, A., Packer, L., Grixti, J.C., Ruz, L., Owen, R.E. & Toro, H. (2005). Increased genetic differentiation in a specialist versus a generalist bee: implications for conservation. *Conserv. Genet.* **6**, 1017–1026.

Zipkin, E.F., Grant, E.H.C. & Fagan, W.F. (2012). Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. *Ecol.*

Appl. **22**, 1962–1972.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**, 3–14.

Figure 1. Occupancy model predictions for European pine martens (*Martes martes*) in Scotland, 2010-2013. Black circles are study sites; each site contained an approximate 4 x 5km grid of ~20 camera-trap stations. We sampled sites up to 800m elevation and comprised of up to 86% agricultural land; predictions extrapolated beyond these values were omitted and are represented in white.


Scotland
N
Aberdeen
Edinburgh
Glasgow
Occupancy probability
1.0
0.0
0
37.5
75
150
Kilometers

1

Figure 2. Associations between occupancy probability and habitat covariates for European pine martens (*Martes martes*) in Scotland, 2010-2013. Black lines are model-averaged mean predictions and gray lines are model-averaged predictions from a random posterior sample of 150-200 iterations to depict uncertainty. Lightly-shaded areas in panels (a) and (d) indicate extrapolative predictions beyond habitat values recorded at study sites (see Supporting Information Table S1).

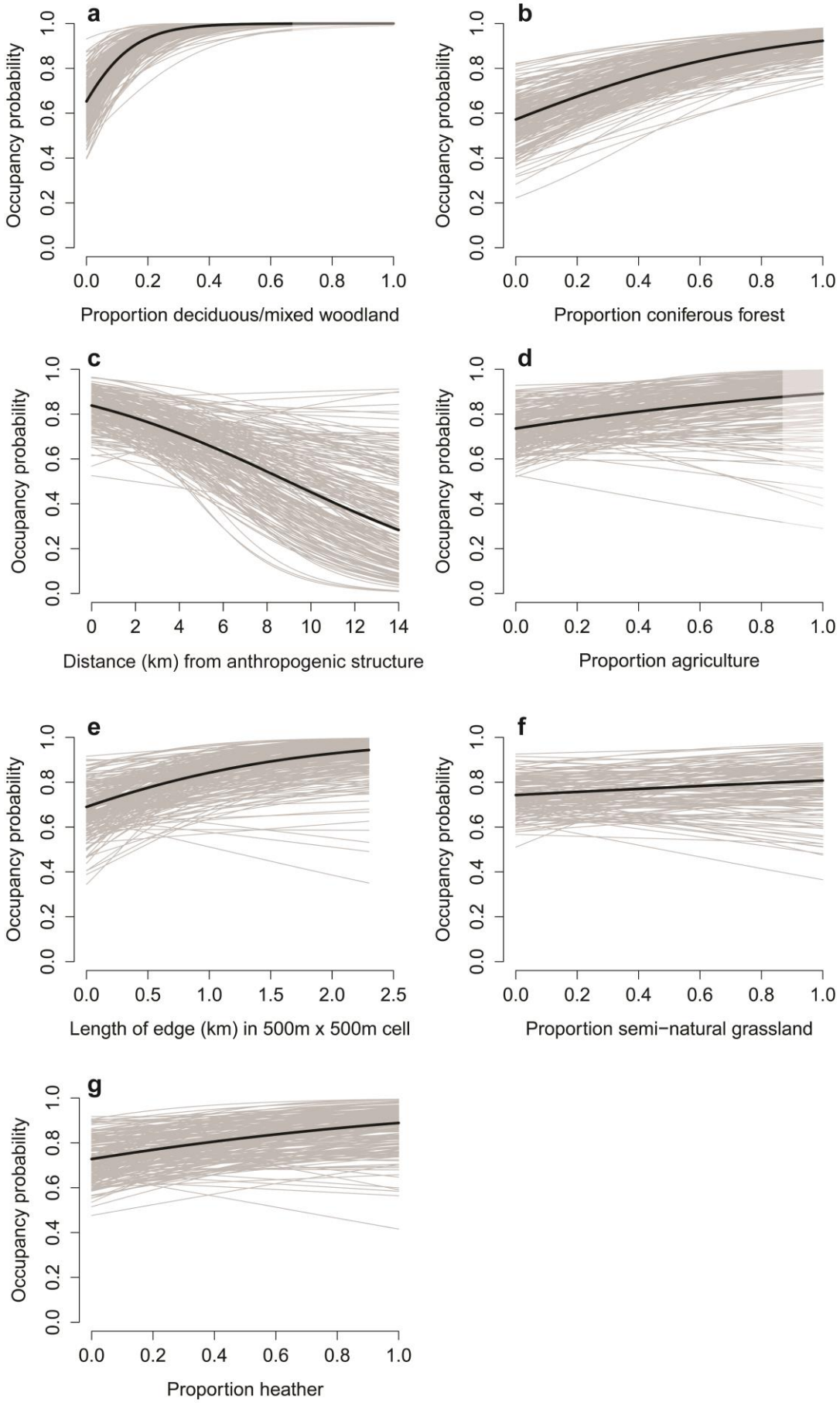

a
Occupancy probability
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Proportion deciduous/mixed woodland
b
Occupancy probability
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Proportion coniferous forest
c
Occupancy probability
0.0 0.2 0.4 0.6 0.8 1.0
0 2 4 6 8 10 12 14
Distance (km) from anthropogenic structure
d
Occupancy probability
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Proportion agriculture
e
Occupancy probability
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.5 1.0 1.5 2.0 2.5
Length of edge (km) in 500m x 500m cell
f
Occupancy probability
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Proportion semi−natural grassland
g
Occupancy probability
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
Proportion heather

Table 1. Habitat covariates, descriptions, and expected associations with European pine marten (*Martes martes*) occupancy probability in Scotland, 2010-2013.

Covariate	Description	Expected association with occupancy	References
agriculture	Proportion agricultural land, including arable cropland and improved grasslands typically comprised of hay meadows and/or grazing pasture.	negative	Balharry 1993; Halliwell 1997; Pereboom et al. 2008; Caryl et al. 2012a; Lombardini et al. 2015
conifer	Proportion coniferous forest, defined as stands with >20% canopy cover formed by coniferous trees that are >5m at maturity. Includes both semi-natural stands (i.e., Scots pine *Pinus sylvestris*) and plantations of both native and non-native conifers (i.e., larch *Larix* spp. and/or spruce *Picea* spp.).	positive	Balharry 1993; Storch 1990, Caryl et al. 2012a; Lombardini et al. 2015
edge	Length of edge (km) between open (heather, semi-natural grassland, and gorse) and closed (conifer and woodland) cover types.	positive, positive quadratic	Pereboom et al. 2008; Mergey et al. 2011; Caryl et al. 2012a

sgrassland	Proportion semi-natural grassland, dominated by largely unmanaged grasses and herbs inhabiting wide range of soil types (i.e., neutral, acidic, and calcareous grasses and herbs; see Jackson 2000 for detailed descriptions).	negative, neutral, or positive	Balharry 1993; Caryl et al. 2012a
heather	Proportion heather and heather grassland, characterized by >25% cover of heath plants (Family Ericaceae).	negative or neutral	Balharry 1993; Caryl et al. 2012a
structure	Cost-distance (km) to nearest anthropogenic structure, including urban and rural settlements as well as farm buildings, retail parks, and urban parkland.	neutral or positive	Birks et al. 2005; Pereboom et al. 2008; Lombardini et al. 2015; Larroque et al. 2016
woodland	Proportion deciduous or mixed woodland, defined as stands with >20% canopy cover formed by trees that are >5m at maturity and comprised of >20% broadleaved trees. Also includes scrub	positive	Balharry 1993; Halliwell 1997; Caryl et al. 2012a; Baines et al. 2013

	vegetation with woody vegetation usually <5m with >30% canopy cover and >0.25ha patch size.

1

Table 2. Occupancy model parameter estimates and detection probabilities for European pine martens (*Martes martes*) in Scotland, 2010-2013.

Parameter	Covariate/description	Mean	SD	95% CI	Inclusion probability
μ of α_{site}	mean of random intercept	1.12	0.44	0.32, 2.07	n/a
σ^2 of α_{site}	variance of random intercept	1.83	0.44	1.16, 2.84	n/a
α_1	agriculture$_i$[1]	0.19	0.19	-0.16, 0.58	0.04
α_2	conifer$_i$	0.78	0.23	0.37, 1.28	0.98
α_3	edge$_i$	0.37	0.22	-0.05, 0.79	0.10
α_4	sgrassland$_i$	0.08	0.15	-0.16, 0.40	0.02
α_5	heather$_i$	0.23	0.18	-0.11, 0.65	0.04
α_6	structure$_i$	-0.45	0.27	-1.01, 0.02	0.12
α_7	woodland$_i$	1.01	0.27	0.55, 1.59	1.00
p	detection probability[2]	0.17	0.01	0.15, 0.19	n/a
q	detection probability[3]	0.41	0.02	0.38, 0.44	n/a
z	stations occupied (out of 526)	337.45	8.48	322.00, 355.00	n/a

[1]The subscript *i* represents camera-trap station; see text and Table 1 for habitat covariate descriptions.

[2]Detection probability for the first survey replicate and all subsequent replicates not preceded by a detection.

[3]Detection probability given a detection during the previous survey replicate.

Supporting Information

Figure S1. Study site locations and habitat rasters depicting the Scottish Highlands, 2010-2013. Black circles are camera-trap study sites (N = 27). For each map, darker colors indicate higher values. All maps depict proportion habitat type ranging from 0-1 except "Edge" (amount of edge in km) and "Urban" (cost-distance to nearest urban or suburban structure in km). Cell size for all rasters was 0.25km^2. See Method and Materials and Table 1 for additional details.

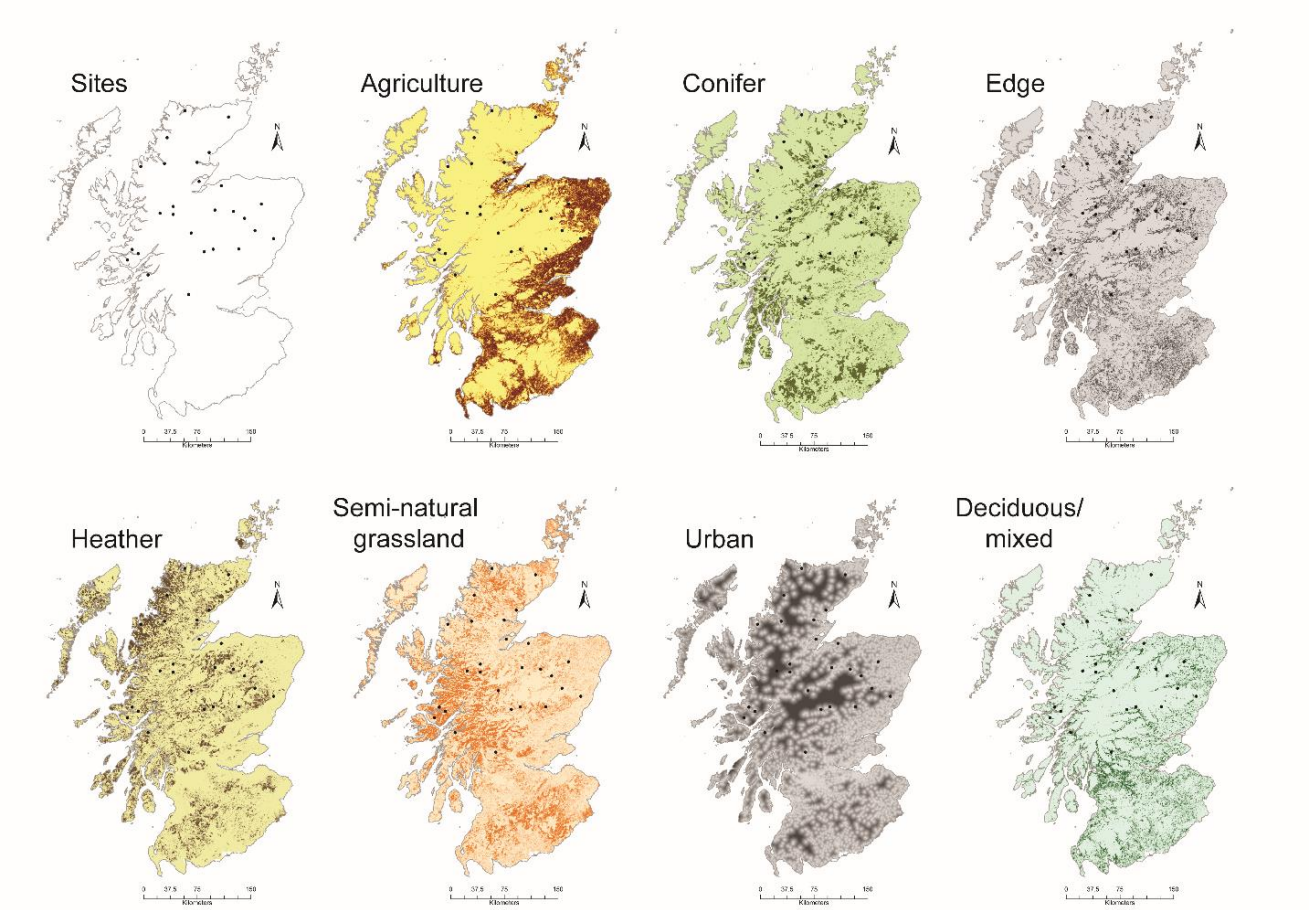


Table S1. Site and camera-trap station descriptions for research conducted in the Scottish Highlands, 2010-2013. Mean, standard deviation, and range of values for each habitat covariate by site. Proportions are proportions of habitat in 0.25km^2 cells containing camera-trap stations at a given site. Distance to urban/suburban structure was generated using a cost-distance raster (see Method and Materials). See Table 1 for covariate descriptions. Values are mean(sd), range.

Site	No. camera-trap stations	Proportion agriculture	Proportion coniferous woodland	Amount of edge (km)	Proportion semi-natural grassland	Proportion heather	Distance to urban/suburban structure (km)	Proportion deciduous/mixed woodland
1	20	0.06(0.17), 0-0.76	0.40(0.36, 0-1	0.06(0.13, 0-0.56	0.11(0.18), 0-0.54	0.02(0.04), 0-0.14	2.59(1.07), 0.82-4.51	0.00(0.01), 0-0.06
2	20	0.11(0.16), 0-0.53	0.86(0.19, 0.44-1	0.13(0.23, 0-0.86	0.02(0.03), 0-0.10	0.01(0.02), 0-0.11	2.08 (0.61), 0.97-3.15	0.00(0.00), 0-0
3	20	0.21(0.22), 0-0.62	0.20(0.31, 0-0.94	0.19(0.29, 0-0.94	0.28(0.28), 0-1	0.14(0.17), 0-0.50	3.82(1.55), 1.32-6.73	0.03(0.06), 0-0.16
4	20	0.26(0.29), 0-0.80	0.62(0.31, 0.12-1	0.34(0.49, 0-2.08	0.06(0.08), 0-0.26	0.00(0.01), 0-0.02	1.40(0.71), 0.08-2.83	0.04(0.07), 0-0.24
5	20	0.06(0.16), 0-0.52	0.32(0.31, 0-0.93	0.30(0.58, 0-2.27	0.39(0.35), 0-0.97	0.15(0.18), 0-0.61	2.58(1.32), 0.41 -5.07	0.05(0.15), 0-0.65

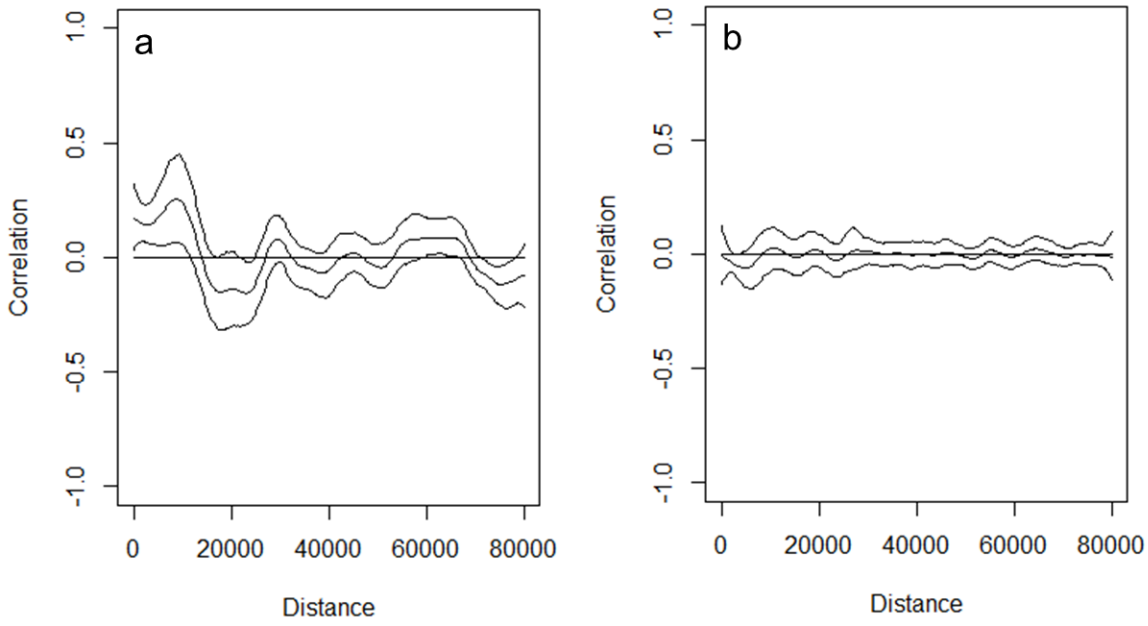
6	20	0.12(0.17), 0-0.55	0.42(0.36, 0-0.98	0.39(0.38, 0-1.31	0.09(0.09), 0-0.24	0.29(0.35), 0-1	1.27(0.67), 0.19-2.53	0.01(0.01), 0-0.06
7	20	0.07(0.13), 0-0.46	0.21(0.28), 0-0.80	0.33(0.33, 0-1.05	0.07(0.09), 0-0.32	0.11(0.16), 0-0.57	3.38(1.03), 1.62-5.30	0.02(0.05), 0-0.15
8	20	0.06(0.12), 0-0.39	0.42(0.35), 0-1	0.24(0.21, 0-0.62	0.21(0.25), 0-0.88	0.24(0.27), 0-0.95	4.50(1.00), 2.56-6.32	0.05(0.09), 0-0.30
9	20	0.12(0.18), 0-0.54	0.57(0.34), 0-1	0.38(0.38, 0-1.24	0.09(0.19), 0-0.62	0.05(0.10), 0-0.35	3.44(1.06), 1.64-5.03	0.04(0.09), 0-0.37
10	20	0.23(0.30), 0-0.84	0.43(0.30), 0-0.91	0.43(0.43, 0-1.47	0.11(0.13), 0-0.45	0.02(0.04), 0-0.13	1.86(0.79), 0.08-3.03	0.12(0.11), 0-0.34
11	20	0.04(0.11), 0-0.37	0.55(0.26), 0-1	0.64(0.50, 0-1.76	0.14(0.18), 0-0.58	0.06(0.12), 0-0.52	3.37(1.34), 0.91-5.26	0.01(0.03), 0-0.11
12	20	0.28(0.25), 0-0.86	0.30(0.28), 0-0.90	0.41(0.24, 0.05-0.98	0.31(0.25), 0.03-0.81	0.05(0.09), 0-0.29	2.61(1.20), 0.70-4.76	0.03(0.05), 0-0.17
13	20	0.07(0.15), 0-0.46	0.54(0.40), 0-1	0.41(0.49, 0-1.92	0.06(0.11), 0-0.42	0.10(0.14), 0-0.44	2.60(1.17), 0.85-4.67	0.02(0.03), 0-0.10
14	20	0.01(0.02), 0-0.06	0.48(0.35), 0-0.96	0.53(0.42, 0-1.78	0.26(0.27), 0-0.86	0.10(0.10), 0-0.30	2.22(0.93), 0.07-3.80	0.04(0.11), 0-0.37
15	20	0.01(0.05), 0-0.20	0.02(0.06), 0-0.21	0.25(0.42, 0-1.25	0.05(0.09), 0-0.32	0.21(0.29), 0-0.91	2.52(1.77), 0.09-6.06	0.06(0.09), 0-0.26

16	20	0.01(0.05), 0-0.21	0.00(0.01), 0-0.05	0.13(0.26, 0-0.83	0.31(0.26), 0-0.76	0.41(0.37), 0-0.91	1.50(0.86), 0.04-3.36	0.03(0.08), 0-0.33
17	20	0.03(0.06), 0-0.22	0.08(0.14), 0-0.38	0.29(0.44, 0-1.42	0.15(0.23), 0-0.83	0.16(0.26), 0-0.97	2.46(1.33), 0.52-4.74	0.09(0.17), 0-0.50
18	20	0.07(0.16), 0-0.67	0.48(0.29), 0-0.94	0.72(0.50, 0-1.64	0.09(0.10), 0-0.29	0.14(0.21), 0-0.77	1.45(0.53), 0.53-2.48	0.05(0.09), 0-0.35
19	20	0.03(0.07), 0-0.22	0.50(0.30), 0.04-0.99	0.70(0.41, 00.6-1.57	0.17(0.16), 0-0.60	0.12(0.19), 0-0.73	2.69(1.05), 0.86-4.48	0.03(0.06), 0-0.28
20	20	0.01(0.03), 0-0.11	0.10(0.23), 0-0.91	0.30(0.41, 0-1.38	0.13(0.19), 0-0.62	0.24(0.30), 0-1	3.80(2.08), 0-6.93	0.11(0.17), 0-0.53
21	21	0.14(0.25), 0-0.77	0.45(0.40), 0-1	0.12(0.17, 0-0.55	0.06(0.12), 0-0.40	0.05(0.12), 0-0.43	1.83(1.18), 0.21-4.20	0.08(0.13), 0-0.41
22	20	0.10(0.22), 0-0.73	0.50(0.39), 0-1	0.42(0.39, 0-1.25	0.09(0.19), 0-0.71	0.04(0.09), 0-0.35	3.65(2.74), 0.09-8.51	0.06(0.09), 0-0.38
23	20	0.00(0.00), 0-0.02	0.08(0.17), 0-0.48	0.23(0.46, 0-1.38	0.34(0.27), 0-0.86	0.18(0.23), 0-0.72	12.67(0.72), 11.19-13.86	0.03(0.06), 0-0.16
24	20	0.09(0.19), 0-0.64	0.31(0.28), 0-0.93	0.36(0.40, 0-1.61	0.03(0.05), 0-0.21	0.14(0.24), 0-0.90	1.45(0.81), 0.16-3.05	0.08(0.12), 0-0.47
25	4	0.07(0.14), 0-0.28	0.35(0.40), 0.02-0.86	0.64(0.59, 0.17-1.47	0.11(0.07), 0.03-0.16	0.04(0.04), 0.01-0.08	0.82(0.56), 0.32-1.61	0.06(0.08), 0-0.16

26	20	0.02(0.06), 0-0.20	0.47(0.33), 0-1	0.67(0.47, 0-1.51	0.24(0.24), 0-0.80	0.08(0.14), 0-0.47	1.21(0.76), 0.16-2.75	0.10(0.17), 0-0.58
27	21	0.01(0.03), 0-0.12	0.61(0.30), 0.10-1	0.41(0.32, 0-1.01	0.10(0.20), 0-0.73	0.10(0.12), 0-0.47	2.22(0.99), 0.64-4.05	0.04(0.08), 0-0.30
	Total	0.08(0.14), 0-0.86	0.38(0.29), 0-1	0.37(0.38, 0-2.27	0.15(0.17), 0-1	0.12(0.16), 0-1	2.81(1.10), 0-13.86	0.05(0.08), 0-0.65

13

Figure S2. Spline correlograms for occupancy models of pine martens in the Scottish Highlands, 2010-2013. Spline correlograms from a generalized linear model (a) and a generalized linear mixed model that included a random intercept at the site level (b) showing a reduction in spatial autocorrelation. Distance is the distance between paired sample locations in meters.



Appendix S1. JAGS code for a hierarchical occupancy model of pine martens in the Scottish Highlands, 2010-2013.

JAGS model code.

```
    model {

    # Occupancy model habitat covariate priors
    alpha1 ~ dunif(-10,10)
    alpha2 ~ dunif(-10,10)
    alpha3 ~ dunif(-10,10)
    alpha4 ~ dunif(-10,10)
    alpha5 ~ dunif(-10,10)
    alpha6 ~ dunif(-10,10)
    alpha7 ~ dunif(-10,10)

    # Inclusion parameter priors
    for (c in 1:7){
    w[c] ~ dbern(0.5)}

    # Detection model priors
    p ~ dunif(0,1)
    q ~ dunif(0,1)

    # Random intercept for each of k sites
```

```
1       for (k in 1:27){
2       int[k] ~ dnorm(mu.int, tau)
3       }
4
5       # Hyperpriors for random intercept
6       mu.int ~ dnorm(0,0.001)
7       tau <- pow(sigma,-2)
8       sigma ~ dunif(0,10)
9
10      # Likelihood model; indexed by camera-trap station (i)
11      for (i in 1:R) {
12      # True state model for the partially observed true state
13      z[i] ~ dbern(psi[i])
14      logit(psi[i]) <-
15      int[site[i]] +
16      w[1] * alpha1 * agriculture[i]  +
17      w[2] * alpha2 * conifer[i] +
18      w[3] * alpha3 * edge[i] +
19      w[4] * alpha4 * sgrassland[i] +
20      w[5] * alpha5 * heather[i] +
21      w[6] * alpha6 * structure[i] +
22      w[7] * alpha7 * woodland[i]
23
```

```
1       # Observation model for detection/non-detection data
2       # First survey
3       y[i,1] ~ dbern(p.eff[i,1])
4       p.eff[i,1] <- z[i] * p
5
6       # All subsequent surveys (indexed by j)
7       for (j in 2:T) {
8       y[i,j] ~ dbern(p.eff[i,j])
9       p.eff[i,j] <- z[i] * ((1-y[i,(j-1)]) * p + y[i,(j-1)] * q)
10      } #j
11      } #i
12
13      # Total number of sites occupied
14      occ.fs <- sum(z[])
15      }
16
17
```