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Estimating distribution and connectivity of recolonizing American marten in the northeastern United States using expert elicitation techniques

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Abstract

The American marten *Martes americana* is a species of conservation concern in the northeastern United States due to widespread declines from over-harvesting and habitat loss. Little information exists on current marten distribution and how landscape characteristics shape patterns of occupancy across the region, which could help develop effective recovery strategies. The rarity of marten and lack of historical distribution records are also problematic for region-wide conservation planning. Expert opinion can provide a source of information for estimating species–landscape relationships and is especially useful when empirical data are sparse. We created a survey to elicit expert opinion and build a model that describes marten occupancy in the northeastern United States as a function of landscape conditions. We elicited opinions from 18 marten experts that included wildlife managers, trappers and researchers. Each expert estimated occupancy probability at 30 sites in their geographic region of expertise. We, then, fit the response data with a set of 58 models that incorporated the effects of covariates related to forest characteristics, climate, anthropogenic impacts and competition at two spatial scales (1.5 and 5 km radii), and used model selection techniques to determine the best model in the set. Three top models had strong empirical support, which we model averaged based on AIC weights. The final model included effects of five covariates at the 5-km scale: percent canopy cover (positive), percent spruce-fir land cover (positive), winter temperature (negative), elevation (positive) and road density (negative). A receiver operating characteristic curve indicated that the model performed well based on recent occurrence records. We mapped distribution across the region and used circuit theory to estimate movement corridors between isolated core populations. The results demonstrate the effectiveness of expert-opinion data at modeling occupancy for rare species and provide tools for planning marten recovery in the northeastern United States.

Introduction

Several species of forest carnivore were extirpated from the northeastern United States in the past two centuries as a result of unregulated harvest and habitat loss due to the expansion of agriculture, livestock farming and development (Gibilisco, 1994). As large tracts of mature forest re-established in the region, some of these species recolonized both naturally and through translocation (Foster *et al.*, 2002). One such species, the American marten *Martes americana*, is considered an indicator of late seral forest health and deep snow pack, and acts as an umbrella species whose conservation supports habitat conditions for a suite of other species (Lambeck, 1997; Carroll, 2007). Martens historically ranged from Alaska, USA, to Newfoundland, Canada, as far north as the tree line and as far south as West Virginia, USA (Krohn, 2012). Unregulated harvest and deforestation caused a significant range contraction in the northeastern United

States during the early 1900s (DiStefano *et al.*, 1990; Gibilisco, 1994; Krohn, 2012). Population recovery is a priority for the northeastern United States and for the states of New Hampshire and Vermont in particular, where the marten is considered threatened and endangered, respectively (New Hampshire Department of Fish and Game 2015; Vermont Wildlife Action Plan Team 2015).

Historically, estimates of marten distribution in the northeastern United States relied on anecdotal reports and occurrence records such as sightings and harvest locations (Hagmeier, 1956; Godin, 1977). These records suggest that by the 1930s, marten were restricted to the mountainous regions of northern Maine and the High Peaks of the Adirondack Mountains in New York (Clark *et al.*, 1987). However, recent genetic data suggest that multiple undetected populations persisted throughout the 20th century in the western Adirondacks, New Hampshire, and perhaps southern Vermont (Fig. 1; C.M. Aylward, J.D. Murdoch & C.W. Kilpatrick, in review). Furthermore, systematic surveys following a reintroduction effort in southern Vermont failed to detect a population that is now understood to have persisted at the time (Moruzzi *et al.*, 2003; C.M. Aylward, J.D. Murdoch & C.W. Kilpatrick, in review). Populations appear to have expanded since the mid-20th century (Fig. 1; Kelly, Fuller & Kanter, 2009; Paul Jensen pers. comm.). However, marten have not been systematically surveyed in the northeastern United States, and trapping localities alone may not be sufficient to provide accurate estimates of distribution. Models that estimate landscape quality may provide better estimates of distribution for this elusive forest-dependent carnivore.

Understanding how landscape quality influences a species distribution, movements and population parameters is essential to achieve recovery objectives. Identifying parcels of land that can potentially support viable populations may help prioritize recovery efforts (Early, Anderson & Thomas, 2008). When these areas are patchily distributed, increasing connectivity with movement corridors may facilitate dispersal and increase the probability of gene flow (Beier & Noss, 1998; Hilty, Lidicker & Merenlender, 2006). Typically, models constructed from empirical data are used to describe habitat quality and connectivity across landscapes (MacKenzie *et al.*, 2002). However, the majority of habitat research on marten has been conducted in core population areas, which are dominated by continuous spruce-fir forest habitat (Bowman & Robitaille, 1997; Godbout & Ouellet, 2010). In the northeastern United States, at the southern periphery of marten distribution, habitat conditions are patchy and martens occupy areas dominated by deciduous or mixed deciduous/coniferous forest. Therefore, habitat selection models derived from core populations likely will not extrapolate well to peripheral populations where martens make use of suboptimal and differential habitat conditions (see Hoffman & Blows, 1994). Moreover, empirical records from the northeastern United States are collected at the township level, which may be too coarse-scale to directly estimate habitat selection models. Recent genetic data also suggest that populations in the northeastern United States persisted for several decades where no empirical records existed, indicating that records of detection may not sufficiently represent the range of occupied habitats (C.M. Aylward, J.D. Murdoch & C.W. Kilpatrick, in review).

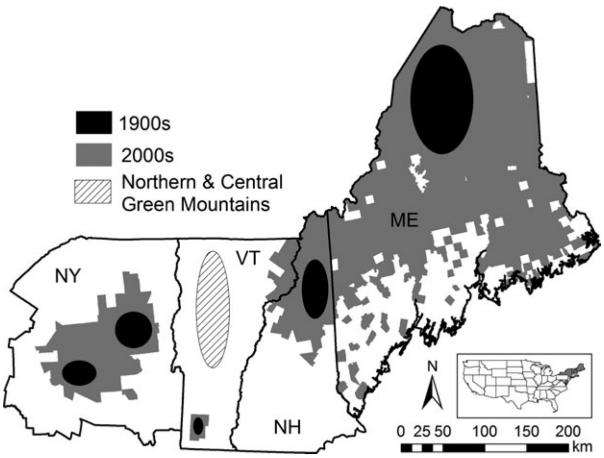

Figure 1 Distribution of American marten *Martes americana* in New York (NY), Vermont (VT), New Hampshire (NH) and Maine (ME) in the northeastern United States (inset) since 2000 based on occurrence records and approximate location of contracted populations in the 1900s based on occurrence records (Hagmeier, 1956; Kelly *et al.*, 2009; Paul Jensen pers. comm.) and inferences from genetic data (C.M. Aylward, J.D. Murdoch & C.W. Kilpatrick, in review).

Due to the uncertainties associated with empirical data in the northeastern United States, and the high cost of obtaining such data, an alternative approach is needed to estimate landscape quality for marten at their southern periphery. Expert opinion can serve as a valuable alternative source of information when empirical data are lacking (Murray *et al.*, 2009). Recent advances in analytical techniques using expert-opinion data allow for stand-alone models to be built, with the flexibility of combining expert-opinion and empirical data to increase robustness of habitat quality estimates (James, Low Choy & Mengersen, 2010; Low Choy *et al.*, 2012).

Our objectives were to (1) Administer a survey to allow for the elicitation of expert opinion regarding factors influencing marten habitat quality; (2) Develop an expert-based occupancy model that describes habitat quality for marten throughout the northeastern United States, accounting for variation in expert opinions and individual expert biases; (3) Use the model to estimate probability of occurrence throughout the northeast; and (4) Estimate connectivity between isolated core areas of marten occurrence in the region.

Materials and methods

Objective 1: expert-opinion survey

To elicit expert opinion, we used an online survey tool developed by the Vermont Cooperative Fish and Wildlife Research Unit based on James *et al.* (2010)'s Elicitator framework (J. Katz & T. Donovan in prep.). The survey tool allowed experts to record their estimates of probability of marten occupancy at a set of randomly selected sites in the northeastern United States. Experts were identified from recent literature and recommendations by state biologists or other experts. Surveys were conducted in-person or via tele- or video conference and user guides were developed to aid experts during the survey.

The expert elicitation approach consisted of four main sections. In section 1, experts completed a pre-survey questionnaire that captured basic information related to their background, such as trapping experience, scientific experience and the relative contributions of field experience and literature to their expertise. In section 2, experts chose their geographic region(s) of expertise at the state level. States included New York, Vermont, New Hampshire, and Maine, which collectively defined the study area (~183 575 km^2, Fig. 1). A set of 30 survey sites, spatially separated by a minimum of 3 km, was then generated in the expert's self-identified region of expertise. A site was defined as a ~7 km^2 circular area (1.5 km radius) – a conservatively large estimate of a male marten home range in northeastern North America (Fuller & Harrison, 2005; Broquet *et al.*, 2006). To maximize the variability of habitat conditions presented to each expert, sites were randomly selected from multivariate iterative-self organizing (ISO) clusters (ESRI 2012); each pixel (30 × 30 m) in the study area was assigned to one of 30 multivariate clusters based on variables provided in Table 1, and one site was randomly selected within each cluster. In section 3, experts were presented with a satellite-view map (Google, Inc., Mountain View, CA, USA) of each site, along with data on twelve covariate values associated with the site (Table 1). Candidate covariates were identified from literature regarding marten habitat selection in the northeastern United States, and Quebec and Labrador, Canada. Covariates for which spatial data were available at the full extent of our study area and <1 km resolution (range = 30–800 m) were used in the survey. For each site, experts estimated the mean probability of marten occupancy (0.0–1.0 scale) and a measure of uncertainty (standard deviation), given the satellite image and covariate information. Section 4 consisted of a post-survey questionnaire to obtain feedback regarding the elicitation process.

Objective 2: occupancy model

We used a model selection approach to identify the best model for estimating marten probability of occurrence (Burnham & Anderson, 2002). The response variable was the expert-defined probability of occurrence and the predictor variable(s) included one or more covariates (Table 1; we added elevation as an additional covariate *post hoc*). To develop the model set, we classified covariates into four categories: (1) Forest Characteristics, (2) Climate, (3) Anthropogenic Impacts, and (4) Competition (Table 1). Next, covariates that did not exhibit a moderate correlation ($r > 0.4$) with respect to mean estimates of occupancy were removed from the covariate set. Candidate models were developed for each individual category and for combinations of categories. Single category models were developed using an all subsets approach. Multi-category models were developed under the following conditions: (1) to avoid over parameterization, no more than one covariate from a single category was included in each candidate model, and (2) because martens are a forest obligate species, each multi-category model included a Forest Characteristic covariate. A second group of models was constructed using the same procedure with covariate values at a landscape scale consistent with similar forest carnivore studies (5-km radius; Kirk & Zielinski, 2009; Long *et al.*, 2011) to incorporate the potential effect of spatial scale on occupancy estimates.

Each model in the final model set (n = 39 models at both spatial scales; Table 2) was fitted using generalized linear mixed models in the R package lme4 (Bates *et al.*, 2015). For model fitting, some covariate values were rescaled to generally range from 1 to 100: elevation values were divided by 10, total basal area of tree stems (TBA) values were divided by 4, and road density and temperature values were multiplied by 10. Before fitting each model, we assessed correlation of the predictor variables and removed models that had high multicollinearity. We selected a conservative multicollinearity cutoff of VIF (variance inflation factor) <2.5 (see Kock & Lynn, 2012). In each candidate model, habitat covariates were considered fixed effects. To account for variation in expert opinions, random intercepts were estimated for each expert. Models failed to converge when more complex random effects, such as slope effects and random effects related to site geography, were attempted. Models were ranked using Akaike's information criterion (AIC; Burnham & Anderson, 2002).

If multiple competing models had strong empirical support (cumulative AIC weight >0.95), we used two model-averaging approaches. First, we calculated a dot product of occupancy predictions from individual models and the models' respective AIC weights (Buckland, Burnham & Augustin, 1997; Burnham & Anderson, 2002). Second, we model-averaged parameter estimates using the R package MuMIn (Bartoń, 2016). We evaluated performance of the final model using a receiver operating characteristic (ROC) curve (Fielding & Bell, 1997; Eng, 2014). A ROC curve, in the context of this study, estimated how frequently the model made a correct prediction (true positive) over a false prediction (false positive) of occupancy. The area under the curve (AUC) provides a measure of the predictive ability of the model. Thresholds of strong model performance are variable in the literature and typically fall between 70 and 90% (Swets, 1988; Zipkin, Campbell-Grant & Fagan, 2012). We used a threshold of 80%. Data points for the ROC curve were generated by creating a set of 1000 'presence' points randomly within townships where martens have been detected since 2000, and a set of 1000 'absence' points within townships where martens have not been detected since 2000 (Fig. 1).

We further analyzed random effects on the top-ranking models to explore expert-to-expert variation. To elucidate trends in expert opinion within our expert group, we collected information regarding each expert's background with respect to marten expertise. We then estimated the average deviation of an expert's intercepts from fixed intercepts in the top three models. Positive deviations indicate an expert overestimated occupancy relative to other experts, and negative deviations indicate an expert underestimated occupancy relative to other experts. We then conducted two-tailed t-tests between expert

Table 1 Covariates presented to experts during a survey to develop an occupancy model for American marten *Martes americana* in the northeastern United States. Covariates were placed into one of four categories (Forest, Climate, Anthropogenic and Competition) for model fitting. Covariates that demonstrated significant correlation (r > 0.5, indicated with an asterisk) with respect to expert occupancy estimates were considered in the final model set.

Covariate Code	Category	Description and Source	Units	Min	Max	r
Forest	Forest	Amount of area in the site classified as coniferous forest, deciduous forest, or mixed forest land cover (Homer *et al.*, 2015)	Per cent	0	100	0.506*
Conifer	Forest	Amount of area in a site classified as coniferous forest land cover (Homer *et al.*, 2015)	Per cent	0	100	0.109
Deciduous	Forest	Amount of area in a site classified as deciduous forest land cover (Homer *et al.*, 2015)	Per cent	0	100	0.295
Mixed	Forest	Amount of area in a site classified as mixed forest land cover (Homer *et al.*, 2015)	Per cent	0	100	0.309
SpruceFir	Forest	Amount of area in a site classified as spruce-fir forest or mixed spruce-fir/hardwood forest land cover (United States Geological Survey Gap Analysis Program, 2011)	Per cent	0	100	0.567*
Canopy	Forest	Amount of ground area in a site directly covered by tree crowns (Homer *et al.*, 2015)	Per cent	0	92	0.557*
TBA	Forest	Average cross-sectional area of tree stems at breast height per acre in a site (Forest Health Technology Enterprise Team 2014)	ft^2/acre	0	295	0.519*
Age	Forest	Average time since previous disturbance of forest stand(s) in a site (Pan *et al.*, 2015)	Years	0	216	0.097
Temp	Climate	Average daily high temperature in a site during the months of November to March (PRISM, Oregon State University 1980–2010 Normals)	Degrees (C)	−6.7	5	0.570*
Precipitation	Climate	Average monthly precipitation in a site from November to March (PRISM, Oregon State University 1980–2010 Normals)	Approx. cm of snow (given freezing conditions)	41	163	0.229
Elevation[a]	Climate	Average elevation above sea level in a site (National Elevation Dataset 2015)	Meters	0	1913	0.626*
Roads	Anthropogenic	Total length of roads per unit area in a site (State Transportation Agencies 2017)	Km/km^2	0	20.21	0.539*
Fisher	Competition	Probability of fisher *(Pekania pennanti)* occupancy in a site (Long *et al.*, 2011)	Per cent	0	99	0.012

[a]Covariate not presented to experts, but used in model fitting.

deviations grouped based on background information obtained from the pre-survey questionnaire to identify potential drivers of relative over- or underestimation.

Objective 3: distribution map

We used the parameter coefficients from the averaged model to map distribution across the study area. We multiplied each covariate raster by the corresponding parameter coefficient, and then summed resulting rasters to obtain a logit score for each pixel. Logits were transformed to probabilities using the logit link function. We developed the map in ArcGIS (v. 10.1, ESRI, Redlands, CA, USA).

Objective 4: movement corridors

We estimated movement flow between core areas of marten occurrence using a circuit theory approach that treats animal movement across the landscape like movement of current through a circuit of varying resistances (McRae *et al.*, 2008). Core areas were estimated as the 'presence' townships from the ROC analysis. Due to geographic connectivity of core areas in Maine, New Hampshire, and northeastern Vermont, and the unlikelihood of a corridor circumventing New Hampshire and northeastern Vermont to connect Maine with another core area, we limited the analysis to New York, Vermont, and New Hampshire. Resistance between areas was the inverse of squared-occupancy rescaled from 1 (least resistance, highest occupancy) to 100 (most resistance, lowest occupancy) to increase the relative effect of habitat quality over Euclidean corridor distance (McRae *et al.*, 2008). We removed Lake George and Lake Champlain from the resistance raster as we considered them impenetrable to dispersal given their size. First, a current was connected between New York, southern Vermont, and northeastern Vermont/New Hampshire populations to map flow using Circuitscape 4.0 (McRae *et al.*, 2008; McRae, Shah & Edelman, 2016). We then estimated potential movement corridors

Table 2 The full set of evaluated models for American marten *Martes americana* occupancy in the northeastern United States. Models were fit from expert elicitation data using generalized linear mixed modeling, with habitat covariates as fixed effects and random intercept effects for each expert. Each model was tested for significantly correlated variables at two scales (1.5-km radius and 5-km radius) using the variance inflation factor (VIF). If VIF was >2.5 in a model (*), the model was discarded from further evaluation. † indicates the model did not converge.

	VIF			VIF	
Single category models	1.5-km radius	5-km radius	Multi-category models	1.5-km radius	5-km radius
Forest models			Forest + climate models		
Forest	N/A	N/A	Forest + temp	1.261	1.207
SpruceFir	N/A	N/A	Forest + elevation	1.792	2.407
Canopy	N/A	N/A	SpruceFir + temp	2.299	2.199
TBA	N/A	N/A	SpruceFir + elevation	1.384	1.333
Forest + SpruceFir	1.171	1.155	Canopy + temp	1.165	1.140
Forest + canopy	4.118*	9.162*	Canopy + elevation	1.620	2.023
Forest + TBA	2.126	2.582*	TBA + temp	1.047	1.008
SpruceFir + canopy	1.199	1.191	TBA + elevation	2.002	2.008
SpruceFir + TBA	1.114	1.058	Forest + anthro models		
Canopy + TBA	2.663*	2.752*	Forest + roads	1.211	1.477
Forest + SpruceFir + canopy	4.233*	9.456*	SpruceFir + roads	1.260	1.423
Forest + SpruceFir + TBA	2.245	2.845*	Canopy + roads	1.215	1.384
Forest + canopy + TBA	5.251*	9.987*	TBA + roads	1.179	1.213
SpruceFir + canopy + TBA	2.866*	3.176*	Forest + climate + anthro models		
Forest + SpruceFir + canopy + TBA	5.374*†	10.462*†	Forest + temp + roads	1.578	2.009
Climate models			Forest + elevation + roads	1.985	2.610*
Temp	N/A	N/A	SpruceFir + temp + roads	2.640*	2.584*
Elevation	N/A	N/A	SpruceFir + elevation + roads	1.553	1.659
Temp + elevation	1.584	1.470	Canopy + temp + roads	1.558	1.978
Anthropogenic impact models			Canopy + elevation + roads	1.807	2.205
Roads	N/A	N/A	TBA + temp + roads	1.622	2.079
			TBA + elevation + roads	2.243	2.446

between southern Vermont and neighboring populations by creating a cost-distance map using Linkage Mapper 1.1.0 (McRae *et al.*, 2008, 2016). The final corridor map represented all cost-distance values <1000 km. We then used Barrier Mapper to identify areas that contributed the greatest cost to the overall cost-distance of the corridor (McRae *et al.*, 2012). Barrier Mapper uses a moving window along each corridor to estimate the effect of habitat improvement at each pixel on cost-distance of the corridor. Pixels that obtain the highest 'habitat improvement score' are areas where habitat improvement would provide the greatest increase in corridor quality, and are, therefore, assumed to currently represent barriers (McRae *et al.*, 2012).

Results

Objective 1: expert-opinion survey

Eighteen experts participated in the survey and included seven state agency personnel, two federal agency personnel, three university researchers and six furbearer trappers. Experts selected sites in Vermont ($n = 5$), Maine ($n = 4$), New York ($n = 2$), Vermont and New Hampshire ($n = 4$), New Hampshire and Maine ($n = 1$), and Vermont and New York ($n = 2$). Surveys took <2 h to complete for each expert. All experts rated their confidence in their ability to predict marten occurrence in the survey at 3 or above on a 1–5 scale (mean = 3.83). Expert roles included eight scientists, five trappers, two managers, two identified as trappers and managers, and one identified as a community member with significant marten experience. Two experts identified their experience as entirely field-based, nine as mostly field-based, one as mostly literature-based and six as evenly split between field- and literature-based expertise.

Objective 2: occupancy model

Seven covariates exhibited moderate correlation ($r > 0.4$) with expert-defined probability of occupancy and were included in the final model set: percent forest land cover (Forest), percent spruce-fir forest land cover (Spruce-Fir), percent canopy closure (Canopy), total basal area of tree stems (TBA), mean daily high temperature in winter (defined as Nov to Mar; Temp), mean elevation (Elevation) and length of class 1–3 roads per km^2 (Roads; Table 1). These variables accounted for three of the four categories hypothesized to affect marten probability of occurrence. The fourth (Competition) was represented by a single covariate (estimated fisher, *Pekania pennanti*, occupancy) and removed due to limited covariate-mean correlation ($r = 0.01$) and experts' lack of confidence in the covariate's accuracy during site elicitation.

Given these 7 covariates, 19 single category models and 20 combined category models were assessed at each scale

(n = 78 total models; Table 2). Of these, 17 models had significant collinearity and 3 models failed to converge and were dropped from the model set, resulting in a final model set of 58 models (Table 2). Of the 58 total models, three models had strong empirical support and accounted for 97.9% of the total weight of the model set (Table 3). All three models were at the 5-km scale and included covariates from Forest, Climate and Anthropogenic categories: Canopy (positive effect), Spruce-Fir (positive effect), Temperature (negative effect), Elevation (positive effect) and Roads (negative effect; Table 3). Individual covariate effects within each model were significantly different from 0 (Table 4; Fig. 2).

Due to the similarity in AIC scores, we conducted model averaging using two different methods: model-averaging occupancy estimates and model-averaging parameter estimates. Both methods resulted in similar model-averaged parameter values, and therefore, we only report results of the parameter model-averaging technique (Table 4). Averaged estimates were used for all occupancy and connectivity estimates. Model performance was strong for the averaged model. The ROC analysis resulted in an area under the curve of 88.1% (Fig. 3).

Analysis of the random effects from the top three models indicated that experts who characterized their expertise as primarily field-based or entirely field-based had significantly higher occupancy intercept values than experts who identified their expertise as primarily literature-based or equally literature- and field-based ($t = 2.14$, d.f. = 16, $P = 0.048$). Though not statistically significant ($t = 1.94$, d.f. = 13, $P = 0.076$), a trend was also found between experts who classified themselves as trappers and experts who classified themselves as scientists, with trappers having higher occupancy intercept values.

Objective 3: distribution map

Occupancy in the study area ranged from 0.00 to 0.97, with an average of 0.35 among pixels. High-occupancy regions existed in northern Maine, northern New Hampshire and northeastern Vermont, throughout the Adirondack Mountains of New York, in the southern Green Mountain National Forest in Vermont, and patchily along the central and northern Green Mountain spine (Fig. 4).

Objective 4: movement corridors

Circuit analysis estimated high current densities in areas adjacent to core populations, in the central Green Mountains in Vermont, and around Lake George in New York (Fig. 5a). The optimal dispersal corridor between southern Vermont and the Adirondacks was an approximately straight line due west (Fig. 5b; hereafter referred to as the Adirondack corridor). The optimal dispersal corridor between southern Vermont and New Hampshire/Northeastern Vermont traveled north through the central and northern Green Mountains, and then east to northeastern Vermont (Fig. 5b; hereafter referred to as the New Hampshire corridor). The optimal dispersal corridor between New Hampshire/Northeastern Vermont and New York also traveled through the northern and central Green Mountains, and crossed from the central Green Mountains to New York between Lake George and Lake Champlain (Fig 5b; hereafter referred to as the NY-NH corridor; the section from the central Green Mountains to New York is hereafter referred to as the Lake corridor). Cost-weighted distance of the New Hampshire corridor (5448 km) was similar to that of the Adirondack corridor (5621 km). The cost-weighted distance of the NY-NH corridor was much greater (9263 km). The ratio of cost-weighted distance to Euclidean distance (CW/ED) between two core areas is representative of corridor quality (McRae *et al.*, 2008). Higher ratios are indicative of either travel through high-resistance habitat or substantial deviation from straight line travel. The New Hampshire corridor exhibited the lowest CW/ED (44.47), followed by the NY-NH corridor (71.42) and finally the Adirondack corridor (84.56). The Adirondack and Lake corridors were strong barriers (Fig. 5c). Moderate

Table 3 Top ten candidate models for American marten *Martes americana* occupancy in the northeastern United States and respective AIC, ΔAIC, AIC weights, and cumulative AIC scores. Models were developed from expert-opinion data from experts in the northeastern United States. Model covariates were fixed effects in a generalized linear mixed model, where expert-specific random intercept effects were also assessed. Models above the gray line contributed to 95% of the cumulative AIC weight and were used in model averaging.

Fixed effect parameters	Scale	AICc	ΔAIC	AIC Weight	Cumulative AIC Weight
Canopy + temp + roads	5k	415.724	0.000	0.444	0.444
Canopy + elevation + roads	5k	416.155	0.432	0.357	0.801
SpruceFir + elevation + roads	5k	417.545	1.822	0.178	0.979
TBA + elevation + roads	5k	422.827	7.104	0.013	0.992
Forest + temp + roads	5k	425.068	9.344	0.004	0.996
TBA + temp + roads	5k	425.486	9.763	0.003	1.000
Canopy + roads	5k	430.609	14.886	0.0001	1.000
Forest + roads	5k	435.382	19.658	0.0001	1.000
Canopy + temp	5k	443.160	27.436	0.0001	1.000
TBA + temp + roads	1.5k	446.660	30.937	<0.0001	1.000

Table 4 Parameter estimates (β) with upper and lower 95% confidence intervals (CI) for covariate effects in the three top models and an averaged model estimating American marten *Martes americana* occupancy in the northeastern United States based on expert-opinion data.

	Covariates	β	Lower 95% CI	Upper 95% CI
Model 1	Intercept	−5.3268	−8.0707	−2.8117
	Canopy	0.0918	0.0604	0.1264
	Temp	−0.0407	−0.0614	−0.0210
	Roads	−0.1993	−0.2787	−0.1250
Model 2	Intercept	−3.2806	−5.8015	−0.9712
	Canopy	0.0449	0.0105	0.0820
	Elevation	0.0394	0.0200	0.0600
	Roads	−0.2422	−0.3138	−0.1762
Model 3	Intercept	−1.1431	−2.2903	−0.0483
	Spruce-Fir	0.0200	0.0029	0.0377
	Elevation	0.0505	0.0342	0.0684
	Roads	−0.2325	−0.3069	−0.1639
Model averaged	Intercept	−3.8180	−7.6699	0.0340
	Canopy	0.0580	0.0138	0.1279
	Spruce-Fir	0.0036	0.0026	0.0375
	Temp	−0.0184	−0.0609	−0.0205
	Elevation	0.0236	0.0215	0.0647
	Roads	−0.2210	−0.3038	−0.1382

barriers were detected in small sections of the central and northern Green Mountains and between the northern Green Mountains and northeastern Vermont (Fig. 5c).

Discussion

Occupancy model

The American marten is considered a forest obligate species requiring deep snow to outcompete sympatric carnivores (Godbout & Ouellet, 2010; Krohn, 2012). Our expert-based model supports a relationship between marten occupancy and habitat covariates related to forested habitats with deep snow and low road densities. Five covariates were included in the top-ranking expert-opinion models: two forest covariates (canopy cover and spruce-fir), two climatic covariates (temperature and elevation) and one covariate related to anthropogenic effects (road density). Our attempt to quantify sympatric competition was through estimates of fisher occupancy, which is a limiting factor of marten distribution in New Hampshire (Kelly *et al.*, 2009). However, we did not find any relationship between expert-predicted marten occupancy and estimates of fisher occupancy. The fisher model we chose was developed in Vermont (Long *et al.*, 2011) where fishers are widespread, and may not have extrapolated well to the rest of the study

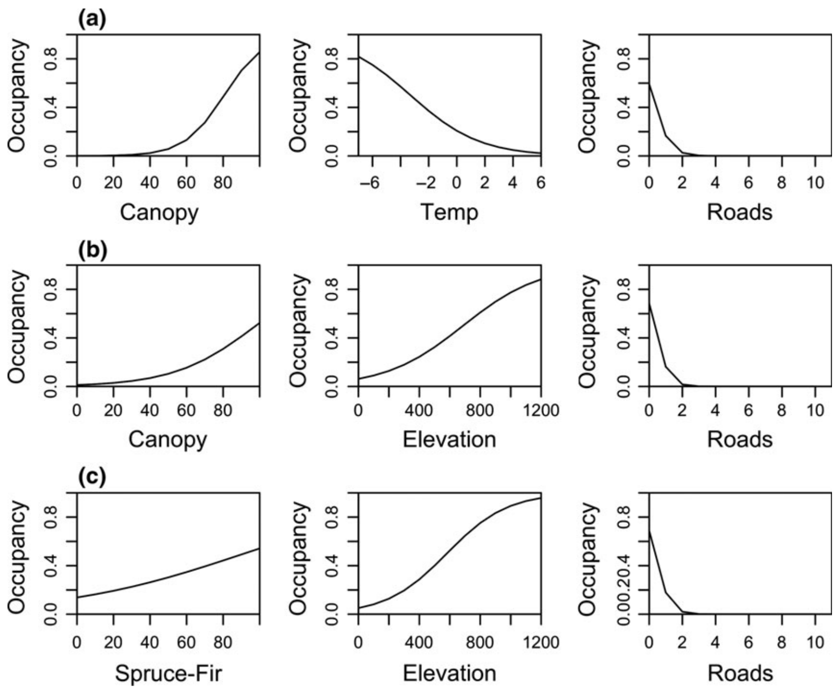

Figure 2 Effects of individual covariates in the top three models (a = Canopy + Temp + Roads; b = Canopy + Elevation + Roads; c = Spruce-Fir + Elevation + Roads) of American marten *Martes americana* occupancy in the northeastern United States. Models were fit by generalized linear mixed modeling based on expert-opinion data. X-axes on plots show the raw habitat covariate values of percent cover (Canopy and Spruce-Fir), degrees Celsius (Temp), km/km^2 (Roads) and meters (Elevation). During model fitting, raw covariate values for elevation, temperature and roads were scaled (divided by 10, multiplied by 2 and multiplied by 10, respectively), and X-axes are back-calculated to show raw covariate values. Y-axes in plots show occupancy probability estimated with other predictor variables in the model held at their mean value in the study area.

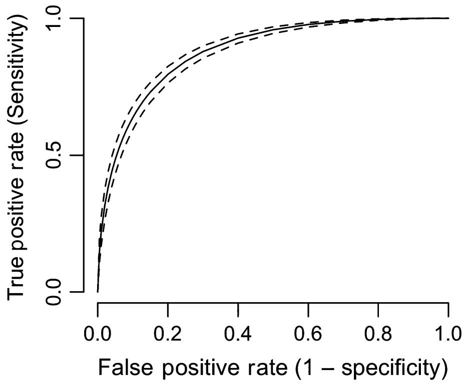

Figure 3 Receiver operating characteristic (ROC) curve obtained from occupancy estimates at 1000 random 'presence' points in townships with recent American marten *Martes americana* detections and 1000 random 'absence' points in townships lacking recent marten detections. The solid line represents the maximum likelihood estimate and dotted lines represent upper and lower 95% confidence limits. The area under the curve (AUC) is 88.1%, indicating strong predictive ability of the model-averaged predictions.

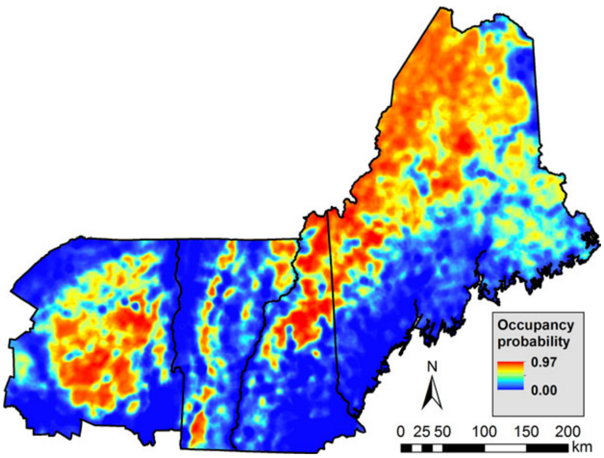

Figure 4 Estimated American marten *Martes americana* occupancy in the northeastern United States based on combined estimates of three models weighted by their AIC weights. Models were fit by generalized linear mixed modeling using expert-opinion data from experts in the northeastern United States. Each expert estimated occupancy at 30 sites using a web-based survey. Expert-specific random intercept effects were combined with fixed habitat effects in each model. [Colour figure can be viewed at https://zslpublications.onlinelibrary.wiley.com]

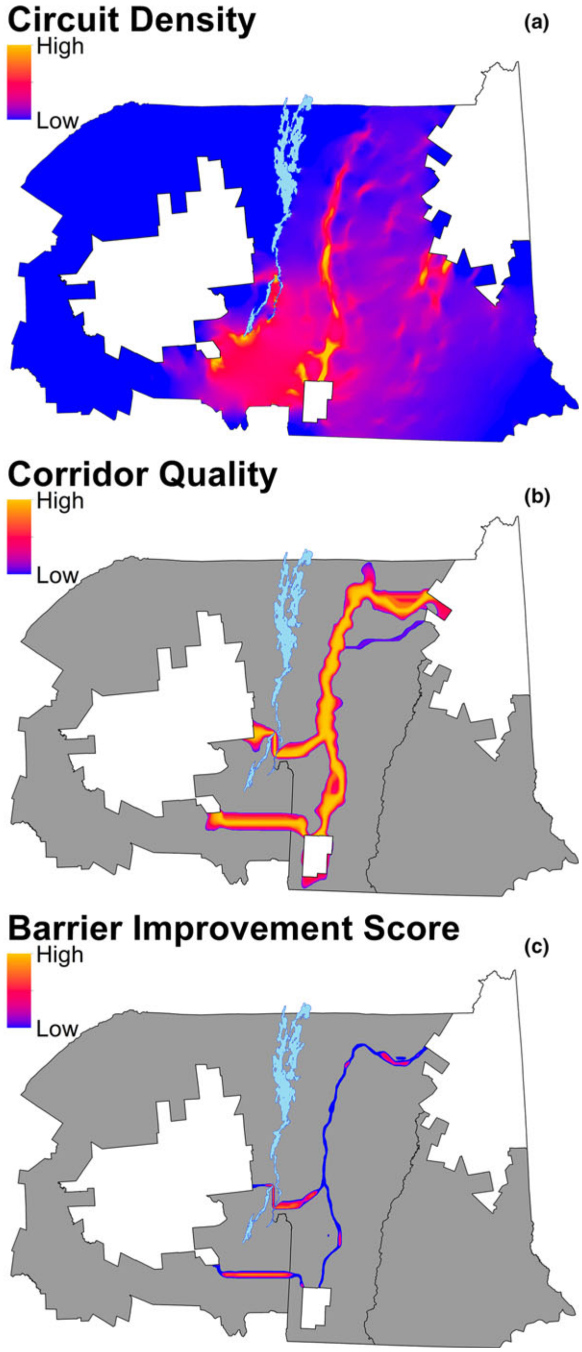

Figure 5 Circuit densities (a), dispersal corridors (b) and corridor barriers (c) estimated for American marten *Martes americana* in southern Vermont and nearby populations (white regions) based on circuit theory and a resistance surface derived from an occupancy model developed from expert estimates of occupancy in the northeastern United States. The occupancy model combined three candidate models weighted by their AIC weights. Models were fit using generalized linear mixed modeling with expert-specific random intercept effects combined with fixed habitat covariate effects. [Colour figure can be viewed at https://zslpublications.onlinelibrary.wiley.com]

area. Studies have also suggested high road densities limit marten distribution as they facilitate movements of larger competitors such as coyotes *Canis latrans* and red fox *Vulpes vulpes* (Sirén, 2009). Consequently, road density may serve as a proxy for competition by other carnivores.

In the core of marten distribution, occupancy and abundance are strongly related to spruce-fir cover (Bowman & Robitaille, 1997; Godbout & Ouellet, 2010). While one of the top models demonstrated this relationship in our study area, the association of occupancy with overall canopy cover (regardless of forest type) in other top models suggests that martens also use mixed and deciduous forest types in our study area. This may be due to availability, as the study area overlays the interface of sub-boreal and northern hardwood habitat types (Foster *et al.*, 2008). In the Turtle Mountains in North Dakota, USA, where spruce-fir forests are unavailable, marten populations are recovering and expanding in forests dominated by deciduous cover (Bagherian *et al.*, 2012). Recent studies show that martens and closely related forest-dependent mustelids persist in irregular, suboptimal or fragmented habitats (see Margey, Helder & Roeder, 2010; Ellington *et al.*, 2017). Populations on the periphery of a species distribution may have increased conservation value due to their adaptations to irregular habitats (Hoffman & Blows, 1994; Lesica & Allendorf, 1995; Channell & Lomolino, 2000). For example, adaptations of martens in our study area to suboptimal habitat conditions, such as mixed northern hardwood forests, may increase the probability of long-term persistence in areas that are anticipated to convert from the preferred spruce-fir habitat to mixed northern hardwood as a result of climate change.

Landscape scale models performed better than home range scale models. This could be a product of a relationship between marten occupancy and large blocks of habitat or bias in expert opinion. Martens are considered a forest interior species, negatively affected by edge effects and subject to predation or competition by larger carnivores that are more closely associated with edge habitat (Kelly *et al.*, 2009; Sirén, 2009). Consequently, there may be a certain distance from edge habitat at which landscape conditions become suitable for martens. As a result, a home range-sized area of otherwise suitable habitat that is surrounded by edge habitat may not support an actual home range. It is also possible that martens occupy home range-sized areas of suitable habitat for short periods of time, but populations are not sustained in these areas. Alternatively, it is possible that expert knowledge of occupancy is biased toward areas that support larger populations. Thus, home range-sized patches that are truly occupied are less likely to be considered high-quality habitat by experts. This would result in a model that performs best at the scale that experts are evaluating habitat, rather than the scale at which martens are selecting habitat. Given the lack of empirical evidence for occupancy in small patches of high-quality habitat, such as the northern and central Green Mountains in Vermont, it is likely that a landscape scale is the appropriate scale to manage marten habitat. In this sense, maintaining large areas of unfragmented high-quality habitat will be important to future marten recovery in the northeastern United States.

Our expert-opinion-based occupancy model predicted marten distribution consistent with contemporary records of occurrence with an area under the ROC curve of 88.1% (Fig. 3). An AUC of 88.1% indicates strong model performance and is consistent with ecological models in similar studies (i.e., Zipkin *et al.*, 2012; Murdoch *et al.*, 2017). Estimates of high occupancy from our model overlapped considerably with records of occurrence in Maine, New Hampshire, New York and southern Vermont (Figs. 1 and 4). In addition, our model suggests that high-quality habitat is dispersed throughout the Green Mountain spine. However, no marten presence has been documented in the northern and central Green Mountains for a century. Anecdotal reports exist from the northern and central Green Mountains, though these are unconfirmed. It is possible that the northern and central Green Mountains are occasionally occupied as dispersal habitat or serve as a metapopulation – supporting temporary subpopulations for brief periods (Hanski, 1998).

A true absence of breeding populations along the Green Mountains despite high habitat quality may be attributed to landscape configuration (Hanski, 2009; Vergara & Armesto, 2009). While high-quality habitat does exist in large quantity in the central and northern Green Mountains, it is primarily arranged in narrow north–south strips following a high elevation (up to 1339 m) spine. In contrast, the occupied areas in southern and northeastern Vermont are plateaus, and habitat quality is not constricted on an axis like in the central and northern Green Mountains. A spine of high-quality habitat may be more subject to pressure from adjacent competitors or predators in the nearby lowlands than a plateau of high-quality habitat. Alternatively, a lack of detections in the central and northern Green Mountains may be a product of sampling bias rather than true absence – also as a result of landscape configuration. Most of the recent detection data from Vermont is a result of incidental trapping in sets for legally harvested species. Reaching the high elevation spine of the central and northern Green Mountains requires more challenging foot travel than the plateaus in southern and northeastern Vermont. As a result, trapping effort may be less intense or non-existent in the high elevations of the central and northern Green Mountains compared with the plateaus.

Expert opinion

Our analysis of random effects revealed a pattern of higher occupancy estimates by experts with field-based knowledge than experts with literature-based knowledge or equal contributions of field- and literature-based knowledge. It is possible that this pattern is driven by the presence of high-quality habitat where no empirical records exist. Experts with field-based expertise may rely on their knowledge of habitat quality and estimate high-occupancy probability in such a site, while experts with literature-based expertise may be hesitant to estimate high-occupancy probability where records do not exist.

We recognize that our modeling approach did not fully account for variation in experts' uncertainty when predicting occupancy at sites. While mixed-effects modeling accounts for relative over- or underestimation of habitat quality among experts, it does not account for variations in confidence among site elicitations within an individual experts' survey (see Low Choy *et al.*, 2012). Plotting standard deviations of experts' site occupancy estimates as a function of estimated mean site occupancy shows that sites of moderate habitat quality resulted in higher levels of uncertainty than sites of extreme high or low quality, where experts were fairly certain about their estimate (Supporting Information Figure S1). An important step for future studies seeking to model habitat quality from expert surveys is capturing the full range of uncertainty, both among experts and within an individual expert's survey. Furthermore, experts recommended that alternative response types (bar plots, numerical entries) would be advantageous for future expert elicitation surveys. Some experts felt distracted by the task of understanding their response as a probability density function and expressed a preference for simply entering a point estimate with upper and lower bounds. Due to variations in expert preferences, either supplying surveys with multiple options or pre-screening experts for their preferred response type could improve the site elicitation process and focus experts' attention to the task of estimating site habitat quality.

Movement corridors

Corridor analysis suggested that the central and northern Green Mountains were the path of least cost-weighted distance between core areas in Southern Vermont and New Hampshire/Northeastern Vermont. In the central Green Mountains, our corridor overlaps with a corridor linking large forest habitat blocks between southern Vermont and northeastern Vermont (Sorenson & Osborne, 2014). However, Sorenson & Osborne (2014) did not identify the northern Green Mountains as important corridor habitat, as our estimate does. The optimal movement corridor between New York and southern Vermont is a nearly straight path that is largely considered a strong barrier. The estimated route travels through extensive low-occupancy agricultural land. Circumventing this area by moving through more forested areas near Lake George is an unfavorable alternative, probably due to the increased travel distance and only limited reduction of travel through low-occupancy areas. Ultimately, the landscape between southern Vermont and New York is extensively low quality such that the optimal dispersal strategy is to minimize travel distance across a uniformly high-resistance matrix. Though these corridors represent the most cost-effective movement paths between core areas, the feasibility of movement or dispersal through them is not evident from these models. Genetic evidence suggests that contemporary gene flow is unlikely between New York and the New England populations, although the southern Vermont and northeastern Vermont/New Hampshire populations may exchange limited gene flow (C.M. Aylward, J.D. Murdoch & C.W. Kilpatrick, in review). It is possible that these corridors are not adequate to functionally facilitate gene flow.

An important consideration to our corridor estimates is the assumption that dispersal habitat quality is directly related to home range habitat quality. While this general relationship probably exists, there is evidence that home range habitat selection and dispersal habitat selection are different in other carnivore species (Palomares *et al.*, 2000; Squires *et al.*, 2013). Studies elsewhere also indicate that gene flow is affected by factors that do not influence occupancy, such as slope (Cushman *et al.*, 2006; Cushman & Lewis, 2010). Consideration should be given to alternative or additional dispersal costs such as total change in elevation, or slope, accumulated over the course of the corridor. In addition, we estimated dispersal habitat based on the top models, which estimated habitat characteristics at a 5-km scale, and corridor selection may occur at a finer scale. Testing hypotheses of dispersal habitat selection will help improve future estimates of movement corridors.

Conclusions

The recovery of marten populations in the northeastern United States has coincided with the re-establishment of older, larger patches of forest habitat (Kelly *et al.*, 2009). Our top models highlighted the positive effect of unfragmented, old-growth forests on marten occupancy. Additionally, the pattern of landscape scale models outperforming home range scale models underscores the importance of maintaining large blocks of high-quality marten habitat. In terms of direct management for martens, our work supports maintaining large blocks of old-growth forest and limiting road development and similar activities that create edge habitat or facilitate movement of larger carnivores. Perhaps, the greatest challenge to marten recovery at the southern periphery of their distribution will be overcoming the negative effects of climate change. Our models show that lower temperatures and higher elevations (both associated with deep snow pack) facilitate marten occupancy. Climate change is expected to increase temperatures and reduce snow pack in the northeastern United States (Carroll, 2007). At the moment, areas that support marten populations at their southeastern periphery may be maintaining snow pack above thresholds that limit densities of competitors. When snow pack thresholds are not met, high canopy cover and low road density alone may not support marten populations. Carnivore communities in the northeastern United States may begin to transition to favor less snow-adapted species, similar to the forest carnivore communities further south, where martens are absent (see Carroll, 2007). A greater understanding of how snow pack, roads and forest characteristics impact interspecific competition between marten and fisher, red fox, and coyote, is important to the recovery of martens in this dynamic landscape. Variation in our occupancy model compared with other models in the core of marten distribution suggests the use of differential habitat conditions, such as the deciduous forests. Martens in our study area may possess particular adaptations to these suboptimal habitat conditions. As landscape conversion occurs in the northeastern United States and southeastern Canada, facilitating gene flow between populations adapted to various habitat conditions will increase the overall resilience of marten populations. An increased understanding of local adaptation to different habitat types will help improve management for adaptive gene flow under conditions of climate change.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Mean and standard deviation (SD) of experts' occupancy estimates of sites from a web-based survey for American marten *Martes americana* occupancy in the northeastern United States. Standard deviation was maximized at moderate mean values and minimized at extreme mean values, demonstrating that perceived habitat quality affected experts' certainty in their estimates.