

# Functional connectivity of lynx at their southern range periphery in Ontario, Canada

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**Abstract** Peripheral populations are often small and isolated compared to those in the range core, in part due to the patchy distribution of suitable habitats at range margins. It follows that peripheral populations typically occur at lower densities and are more susceptible to extinction, but their persistence may be facilitated through connectivity with core areas. Relationships between connectivity and the distribution of animal populations have not yet been fully evaluated, especially for large carnivores having extensive spatial needs and specialized habitat requirements. Using observations of snow tracks, we modeled occurrence of Canada lynx (*Lynx canadensis*) in relation to landscape characteristics along their southern range periphery in Ontario, Canada; we sought to assess functional connectivity of lynx habitat along the southern margins of the range. As observed

in other studies, young coniferous forests had the highest probability of lynx occurrence, likely due to their association with snowshoe hares (*Lepus americanus*). We used the occurrence model to parameterize a resistance surface and then circuit theory to predict functional connectivity along the southern periphery of lynx distribution. Lynx typically travelled through landscapes with higher connectivity than random paths, implying that lynx habitat requirements in their southern range likely extend beyond habitat composition, and that conservation efforts should seek to preserve metapopulation dynamics through functional connectivity of suitable habitat across larger spatial scales.

**Keywords** Landscape resistance · Range periphery · Canada lynx · *Lynx canadensis* · Circuit theory · Occupancy · Functional connectivity · Habitat

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## Introduction

There is increasing and widespread recognition that in order to conserve and manage species effectively, it is necessary to increase links between empirical data and predictive models. An important application of such efforts involves predicting impacts of anthropogenic activities and environmental change on animal populations and their habitats (e.g., Hoegh-Guldberg 1999;

McRae et al. 2008), and identifying areas or species having conservation priority (e.g., Carroll et al. 2001). Generally, empirical habitat models quantify patterns of use by species in relation to a set of relevant environmental characteristics, such as land cover and climate. Habitat composition, however, is not the only factor that influences species occurrence in a landscape. Some seemingly unsuitable habitats may be important if they increase functional connectivity and thereby facilitate movement between habitat patches (e.g., Haddad and Tewksbury 2005; Binzenhöfer et al. 2008). Thus, models of habitat use would benefit by considering functional connectivity in addition to standard measures of habitat composition.

Functional connectivity can be defined as the connectedness of habitat for a particular species (Fischer and Lindenmayer 2007) and refers to landscape characteristics that facilitate or impede movement between resource patches (Taylor et al. 1993). Assessing functional connectivity involves linking the structural characteristics of the landscape with ecological and behavioural characteristics of the species or community of species (Adriaensen et al. 2003). Models that distinguish between habitats of varying quality for a species are prerequisites to estimating functional connectivity because animals are assumed to select movement paths in the same way they choose habitat (Beier et al. 2008). Individuals experience reduced ecological costs (e.g., mortality risk) when moving through favourable habitats (Rayfield et al. 2010), meaning that high quality habitats are assumed to be more permeable to movement than low quality habitats. It follows that assessing cost of movement through a landscape is an important component of assessing connectivity, but true costs of movement are rarely known and often must be estimated from expert opinion or literature review (Chetkiewicz and Boyce 2009). Intuitively, resistance values derived from empirical data should improve the accuracy of predicted habitat corridors because they reflect observed habitat associations of the focal species (Chetkiewicz and Boyce 2009; Rayfield et al. 2010). Occupancy models derived from empirical occurrence data offer a promising source for parameterizing connectivity models, particularly as recent advances in occupancy modeling that incorporate detection probabilities from repeated visits have improved their reliability and accuracy (Mackenzie 2005). Such models assume that the probability of occurrence is

correlated with habitat quality, and that landscape resistance to movement is inversely correlated to habitat quality (Tyre et al. 2001; Chetkiewicz and Boyce 2009). Accordingly, resistance can be assigned values derived from probabilities of occurrence.

Landscape resistance can be applied to assess functional connectivity using least cost path (LCP) analyses, although this identifies only the optimal route and ignores potential alternate paths (Chetkiewicz and Boyce 2009). Taking advantage of similarities between electrical current and random walks (Doyle and Snell 1984), electrical circuit theory has recently been applied as an alternative to LCP. In circuit theory, a landscape is depicted as a network of nodes (raster pixels) connected by edges weighted by their perceived costs (Urban and Keitt 2001; McRae et al. 2008). Landscape resistance to movement is computed by quantifying commute times for random walkers traveling between nodes via edges in the landscape network (McRae et al. 2008). By exploiting circuit theory we can compute effective resistance, voltage, and current which can all be related to movement ecology. Effective resistance is a relative measure of isolation of patches or populations in the landscape. Voltage is an index of successful dispersal by an organism between patches and varies according to the structural landscape and distance. We were interested in identifying habitats that contribute to connectivity however, so we focused on assessing current, which is effective resistance standardized by voltage, and is analogous to the density of random walkers. Areas with high current density would be expected to have a high density of random walkers and hence a high likelihood of animals passing through them (McRae et al. 2008). Although voltage and effective resistance both provide valuable information about how the structural landscape influences functional connectivity, current is particularly useful for predicting corridors and identifying locations that increase functional connectivity. Circuit theory builds upon least cost path analysis by identifying all possible corridors contributing to connectivity between source and destination locations and it can also be applied to make predictions about movement patterns through contiguous landscapes (McRae et al. 2008).

Canada lynx (*Lynx canadensis*) have experienced habitat fragmentation and associated range loss in the southern portion of their distribution in southern Canada and the contiguous United States (U.S. Fish

and Wildlife Service 2000; Poole 2003). The long-term persistence of southern lynx populations may depend on dispersal from core populations in central Canada (Murray et al. 2008) implying that assessing functional connectivity between core and peripheral lynx populations should be a research priority. Lynx rely on snowshoe hare (*Lepus americanus*) as prey, and habitat requirements of both species are closely linked, tending towards early successional forests with heavy understory (Parker et al. 1983; Hoving et al. 2004; Fuller et al. 2007; Vashon et al. 2008b). Other factors can affect lynx occurrence and distribution, for example roads increase lynx mortality risk and may facilitate lynx co-occurrence with competitors like coyotes (*Canis latrans*) and bobcats (*Lynx rufus*; Bayne et al. 2008), whereas snow conditions may preclude lynx spatial overlap with competitors (Murray and Boutin 1991; Buskirk et al. 2000).

We sought to explain patterns of lynx occurrence along their southern range periphery by comparing thirteen models addressing five hypotheses about range limitation in lynx, including: (i) anthropogenic activities (road density and forestry activities), (ii) climate (snow conditions), (iii) forest type, (iv) forest age, and (v) sample year (Table 1). We estimated the probability of lynx occurrence from patterns of lynx tracks observed in the snow, and we parameterized a resistance surface from probabilities of occurrence. We then used circuit theory to predict connections

between core and peripheral habitats across the resistance surface, and to test whether lynx selected connected routes. To our knowledge, this is the first study to examine predictions of functional connectivity derived from empirical occupancy models.

## Methods

### Study area

The study was conducted in a 4,000 km<sup>2</sup> area in central Ontario, east of North Bay between Lake Nipissing and the Ottawa River (Fig. 1). This region is characterized by well drained moraine substrate with pockets of lacustrine deposits, ranging in elevation from 200 to 375 m (Baldwin et al. 2000). We examined lynx habitat relationships along the southern periphery of their range which was generally parallel to the southern edge of the boreal forest. The transition between boreal forest and the Great Lakes forest region was thus centrally located in the study area. The boreal forest is characterized by its cold climate, regular fire disturbances, and paucity of tree species (Thompson 2000). To the south, the Great Lakes forest region has richer tree species diversity, longer growing seasons, and greater annual precipitation (Thompson 2000).

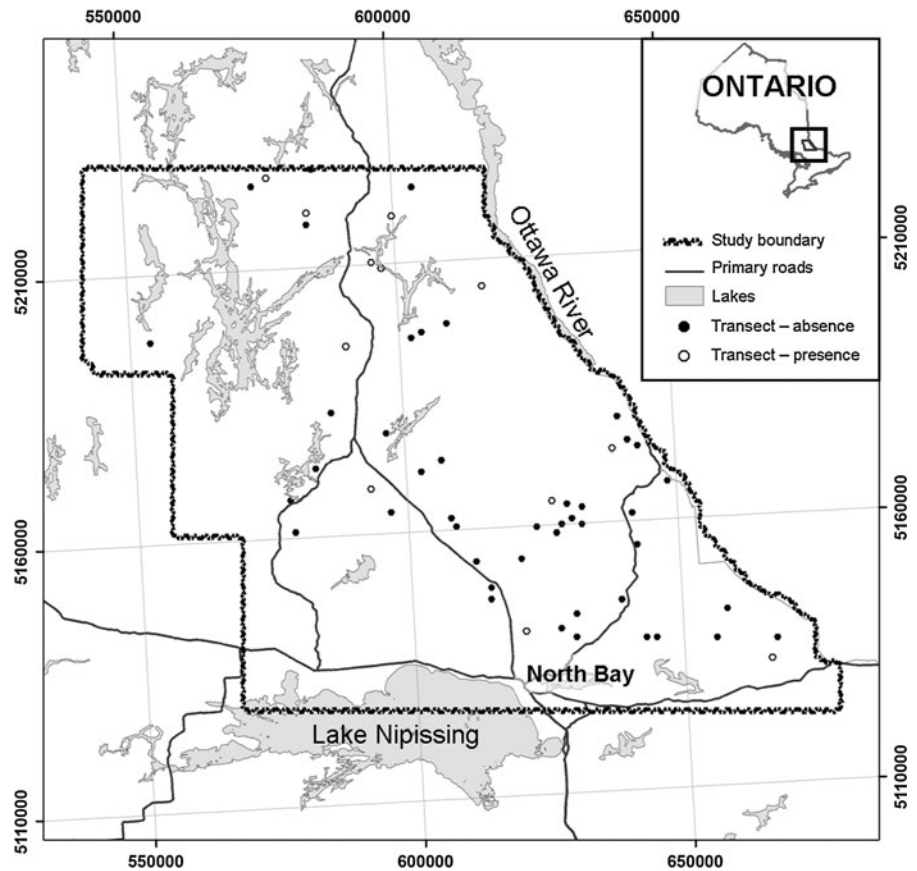
### Field sampling

Winter is an appropriate time to assess functional connectivity for lynx because both natal (i.e., when young are evicted from their natal territory) and environmental (i.e., motivated by nutritional stress) dispersal events generally occur during this period (Poole 2003). It is also a time when snow tracking can be used in northern environments. During winters 2009 and 2010, we searched for lynx sign using snow track surveys along 56 triangular transects. Transects were distributed throughout the study area, were accessible by snowshoe (within 2 km of a road or trail), and were re-sampled between 1 and 4 (mean = 3) times each year between January and March, 2009 and 2010. Each transect was located within a hexagonal shaped cell with an area of 42 ha. Transect locations were chosen in a stratified random fashion to capture the natural variability in forest cover types and forest development stages in the study area. Each transect measured 500 m

**Table 1** Variables tested for influence on Canada lynx (*Lynx canadensis*) occurrence at the southern periphery of their distribution in Ontario, Canada, and predicted direction of relationship

Variable	Predicted direction of relationship	Justification
Distance to roads	Negative	Habitat loss and fragmentation
Proximity to forestry activities	Negative	Habitat loss and fragmentation
Snow conditions	Positive	Competitive advantage
Forest type (proportion conifer)	Positive	Abundant prey
Forest age (proportion young forest)	Positive	Abundant prey
Sample year	No effect	No difference between years

**Fig. 1** Map of a Canada lynx (*Lynx canadensis*) study area in central Ontario, Canada. Detections (presence) and non-detections (absence) of lynx are illustrated for each transect ( $n = 56$ )



per side for a total of 1,500 m (similar to Bayne et al. 2008). Observers snowshoed transects and documented evidence of lynx occurrence (i.e., snow tracks or other sign) within 10 m on either side of the transect. Repeated visits permitted estimation of lynx detection probability. Transects were visited between 6 and 90 h since last snowfall and time since last snowfall was used as a sampling covariate to estimate detectability.

#### Landcover maps

We used information from digitized forest resource inventory (FRI) layers (OMNR unpublished data) in ArcGIS 9.3.1 (ESRI 2009) for habitat modeling. Land cover types were aggregated into coniferous, deciduous, mixed, hemlock (*Tsuga canadensis*), poplar (*Populus* spp.)-birch (*Betula papyrifera*), wetlands, water, or other (Maxie et al. 2010), and forest stand age was aggregated into four development stages: pre-sapling, sapling, immature and mature/old (Holloway et al. 2004; Maxie et al. 2010).

#### Explanatory variables

We measured six variables from which we developed additive models to test our hypotheses about lynx range limitation. Two variables, proportion of coniferous forest and proportion of young forest, were estimated within the 42 ha polygon. The proportion of coniferous and young forest was derived from forest stand characteristics in the FRI. Young forests represented an aggregation of sapling and immature development stages. Sapling development stage generally ranged from 10 to 40 years old. Immature stands ranged from 30 to 80 years old and had little understory development (Holloway et al. 2004). We considered merging these age classes to be appropriate for assessing lynx and hare habitat use (Mowat et al. 2000). Overlap in the age range of sapling and immature trees are a result of species specific differences in ages of maturation. Areas designated as coniferous forest represented an aggregation of Ontario standardized forest units (obtained from the

FRI) containing stands with spruce (*Picea glauca*, *P. mariana*), pine (*Pinus resinosa*, *P. strobus*, and *P. banksiana*), fir (*Abies balsamea*) and cedar (*Thuja occidentalis*) in upland and lowland environments. Many stands included mixtures of pine, fir-spruce, or jack pine-black spruce (Holloway et al. 2004). There were significant positive correlations (all  $r_s > 0.73$ ,  $n = 56$ ,  $p < 0.05$ ) in both the proportion of coniferous forest and the development stage measured across a range of hexagon sizes (42, 87, 195, and 779 ha), suggesting that small areas (e.g., 42 ha) were compositionally similar to large areas (i.e., 779 ha). Subsequent analyses were based on a 42 ha hexagon because this size closely contained the area of our sampled transect while providing a high resolution map.

Snow conditions were measured at each corner along surveyed transects. The snow condition variable was a combination of the total snow depth, crust depth and snow density averaged across the three points of each transect. We used snow measurements from one site visit roughly during mid winter when snow conditions were relatively stable. Early and late winter snow conditions were quite variable due to the frequent and short term thawing events. Total snow depth was the average depth of three measurements from the surface of the snow to the forest floor beneath. Crust depth was the average depth of three measurements from the surface of the snow to the first snow crust layer. Snow density was the density of top layer of snow up to 50 cm. Density was determined by measuring the weight, depth and volume of a core sample collected with a plastic polyvinyl chloride pipe. We regressed the three snow metrics against Julian date and reduced the residual values of the regressions to a single factor score with Principal Component Analysis. Factor 1 score accounted for 62.5% of the variance in the samples and explained a negative effect of crust (eigenvector =  $-0.606$ ) and total snow depth ( $-0.467$ ) and a positive effect of snow density (0.644).

Anthropogenic activities were represented in the modeling by the distance to the nearest road and the nearest forestry operation carried out since 2004. The Euclidean distance from the centroid of each triangle to the nearest road (Ontario Road Network, Ontario Ministry of Natural Resources 2005) and forestry activity was measured with ArcGIS 9.3.1 Spatial Analyst (ESRI 2009).

## Occurrence modeling

We developed occupancy models for lynx following methods established by Mackenzie et al. (2002). We selected thirteen models a priori from additive combinations of the six explanatory variables. The thirteen models were selected because they addressed five candidate hypotheses explaining lynx occurrence along the southern range periphery in Ontario: coniferous cover, forest age, anthropogenic activity, snow, and sample year (Table 3). Although we were primarily interested in occupancy ( $\Psi$ ), we also explored sample covariate effects (e.g., time since last snowfall) on detection probability ( $p$ ). We performed occupancy modeling in Program Presence 2.4 (Hines 2006). Occupancy modeling incorporates imperfect detection into estimates of log likelihood by considering the pattern of detection versus non-detection from repeated surveys. The detection rate is often related to sample occasion or site specific covariates due to variability in an observer's ability to detect sign (e.g., weather, thick understory). It is therefore possible to incorporate varying detection rates into parameter estimates from the contributions of the covariates and encounter histories from multiple site visits. Models where the probabilities of occurrence or detection were assumed constant are denoted with a period,  $\Psi$  (.) or  $p$  (.) respectively.

We ranked the thirteen models of occurrence with Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) based on their ability to predict the observed pattern of lynx detections quantified by  $-2$  log-likelihood estimates with the logit link function. We found no correlations among the explanatory variables (all  $r_s < 0.31$ ,  $n = 56$ ,  $p > 0.05$ ) indicating an absence of multi-collinearity. For the global model we estimated a variance inflation factor,  $\hat{c}$ , that measures the degree of over-dispersion ( $\hat{c} > 1$ ) due to lack of independence in the data (Richards 2008). We found that  $\hat{c} < 1$  for the global model, suggesting no over-dispersion (Hosmer and Lemeshow 2000). The top models were selected based on natural breaks in relative importance values and delta  $AIC_c$  values ( $\Delta i$ ; roughly  $< 2$ ). We model-averaged the top models to calculate weighted parameter estimates and weighted unconditional standard errors and considered variables with confidence intervals that did not overlap zero to be biologically meaningful.

## Lynx occurrence map and model validation

We mapped occurrence probabilities of lynx in the study area based on the model-averaged coefficients from the best ranked models. We tessellated the study area with square grid cells of 0.0225 km<sup>2</sup> (150 m × 150 m), 0.09 km<sup>2</sup> (300 m × 300 m), 0.36 km<sup>2</sup> (600 m × 600 m), and 1 km<sup>2</sup> (1,000 m × 1,000 m) and applied the top model to each cell to calculate probability of lynx occurrence for that cell. We detected a positive correlation in occurrence probabilities across all spatial resolutions of grid cells (all  $r > 0.8$ ,  $p < 0.05$ ). Therefore, we used a pixel size of 0.0225 km<sup>2</sup> for further analysis because this scale improved map resolution and yet was large enough to contain multiple cover types necessary for precise estimates of occurrence probability.

We used a separate dataset of lynx tracks detected opportunistically from surveys along roads and trails during winters 2009 and 2010 to assess the accuracy of modeled lynx occurrence probabilities. We identified 120 random points within a distance of 4 km of surveyed routes, hereafter pseudo-absences, and extracted map probabilities underlying the points for comparison with 38 observed lynx occurrences. Given a valid model, we expected the mean probability of occurrence to be higher where lynx were observed rather than at pseudo-absence points.

## Connectivity modeling

Measuring functional connectivity involves assigning costs to various habitat types that might accrue when traversing the landscape between source and destination nodes. We assigned cost weights based on occurrence probabilities, such that the resistance surface was comprised of a raster of probabilities derived from our model of lynx occurrence. Since our objective was to identify connective landscapes along the southern periphery, we positioned source and destination nodes at the most northern and southern extents of the study area. We were not concerned about possible east–west corridors because our study area was bordered by barriers to the east (Ottawa River) and west (Lake Nipissing; Fig. 1), limiting large scale movement to a north–south orientation. The source and destination nodes were linear bands of pixels traversing the width of the study area from east to west. The nodes were positioned beyond the

northern and southern edges of the study area by approximately 40 km (Fig. 4) to avoid bias due to edge effects (Koen et al. 2010).

We modeled functional connectivity of the southern range periphery of lynx in Ontario using circuit theory (McRae et al. 2008) in Circuitscape 3.5 (Shah and McRae 2008). We compared length-weighted mean current values underlying geo-referenced backtracks of lynx trails to simulated correlated random paths created with Hawth's Analysis Tools (ver. 3.2.7; 2006) to determine if lynx were traveling through cells predicted to have high current (and therefore contribute to functional connectivity). The length-weighted mean current values were calculated by multiplying the length of each segment along the entire path by the raster cell value underlying that segment, summing this value (i.e., current × segment length) across all segments in the path and then dividing the sum by the total length of the path. Simulated random paths ( $n = 100$ ) were approximately equal in length with similar mean turning angles and similar turn angle variation and step length as the average of all the backtracked lynx trails ( $n = 31$ ). If our predictions of functional connectivity were supported, then the length-weighted mean current should be greater along lynx paths than along random paths.

Random points and paths were located within a radius of 4 km (circular area of 50.3 km<sup>2</sup>) of the surveyed trails because a circle of this radius is roughly the size of the lynx home range along the range periphery (Vashon et al. 2008a). Therefore, lynx with home ranges along the surveyed routes would likely have been detected had they been present since the surveys traversed through the theoretical home ranges on multiple occasions (1–4 times each year). As such, we considered the random points and paths used to validate the models as pseudo-absences.

## Results

We visited 56 transects between January and April, 2009 ( $n = 48$ ) and 2010 ( $n = 8$ ); each transect was re-sampled within the same year between 1 and 4 times (mean = 3). Transects were spread throughout the study area with a mean (SE) distance between transects of 45.7 (3.2) km (Fig. 1). Overall, lynx were detected 18 times at 21% ( $n = 12$ ) of transects. Lynx detections occurred among transects that contained a

higher proportion of coniferous and young forests and were farther from recent forest harvest activities compared to that available in the landscape (Table 2).

Climate differed noticeably between the two years. Winter months during 2009 were colder (mean temperature =  $-6.2^{\circ}\text{C}$  in 2009 versus  $-2.6^{\circ}\text{C}$  in 2010,  $p < 0.05$ ) and received more snow compared to 2010 (157 and 87 cm total annual snowfall, respectively). Distance to the nearest road also varied by year (2009: 2.73 km, 2010: 1.32 km), which was an artefact of random sampling and the small sample size in 2010. All other explanatory variables of transects were equal across years.

### Occurrence modeling

We ranked the thirteen occurrence models with AIC<sub>c</sub> and found that those containing variables: (i) young forest, (ii) coniferous forest, and (iii) constant detection probability, best predicted the observed pattern of lynx occurrence at the surveyed sites (Table 3). There was a substantial difference in fit between the third and fourth models, [ $\Psi$  (*Young forest*)  $p$  (.)] and [ $\Psi$  (*Forestry proximity*)  $p$  (.)], respectively. Further, importance weights ( $w_i$ ) suggested that the top three models were between 2.35 and 2.04 times more likely than the fourth-ranked model (i.e., [ $\Psi$  (*Forestry proximity*)  $p$  (.)]) to be the best model explaining lynx occurrence (Table 3). The weighted composite model derived from the top three models indicated that both coniferous forest and young forest had positive coefficients, suggesting that these habitat features had a positive relationship with lynx probability of occurrence; neither estimate overlapped zero (Table 4). The composite model predicted that the mean (SE)

proportion of the sites occupied was 0.38 (0.03). The probability of detecting a lynx (SE) when present at a site was 0.37 (0.17) and was consistent across all survey replicates.

### Occurrence probability map and validation

We applied the composite model of occurrence (Table 4) to land cover within each of the 0.0225 km<sup>2</sup> cells tessellating the study area in ArcGIS 9.3.1 (ESRI 2009). The model predicted that mean occurrence probability for the entire study area was 0.346 (pixel values ranging from 0.156 to 0.929; Fig. 2). In general, the northern (0.410) and central (0.361) portions of the study area had a higher mean probability of lynx occurrence than the southern third (0.271). In particular, the southeastern portion of the study area was dominated by mature deciduous forests and consequently the model predicted a large area with low probability of lynx occurrence (Fig. 2). The mean predicted probability of occurrence underlying lynx points from the independent data set were significantly higher than probabilities underlying pseudo-absence points (Mann–Whitney U test;  $Z = -3.491$ ,  $p = 0.0005$ ; Fig. 3A), which suggests that our occurrence model for lynx accurately predicted their location in the landscape.

### Connectivity modeling

The application of the circuit model demonstrated regions of high current in the north and west of our study area, and a region of low current in the southeast of the area (Fig. 4). There were several different bands of current oriented in a north–south direction that

**Table 2** Descriptive statistics of the explanatory variables at sites representing the study area ( $n = 56$ ) and at sites where Canada lynx (*Lynx canadensis*) were detected ( $n = 12$ )

The time since last snowfall represents averages of repeated visits (1–4 visits)

Explanatory variables	Study area		Lynx detections	
	Mean	SE	Mean	SE
Snow depth (cm)	72.46	2.19	69.53	2.21
Snow density (g/cm <sup>3</sup> )	0.23	0.01	0.23	0.01
Crust depth (cm)	18.30	1.77	19.93	1.77
Proportion conifer forest	0.32	0.04	0.46	0.04
Proportion young forest	0.21	0.04	0.36	0.05
Distance to harvest (m)	5206.48	433.20	6303.00	411.04
Distance to road (m)	2526.38	317.85	2451.38	305.07
Time since last snowfall (h)	109.73	8.12	119.50	18.94

**Table 3** Thirteen candidate occurrence models for Canada lynx (*Lynx canadensis*) in central Ontario, Canada, ranked with Akaike's Information Criteria corrected for small sample size ( $AIC_c$ ), the difference from top  $AIC_c$  model ( $\Delta_i$ ), and model

weights ( $w_i$ ) where  $K$  is the number of parameters in the model,  $N$  is the sample size and  $-2LL$  is the  $-2$  log likelihood estimate used to derive  $AIC_c$

Model	$K$	$N$	$-2LL$	$AIC_c$	$\Delta_i$	$w_i$
$\Psi$ (Coniferous forests) $p$ (.)	3	56	98.00	104.46	0.000	0.21
$\Psi$ (Young forest, Coniferous forest) $p$ (.)	4	56	95.97	104.75	0.290	0.18
$\Psi$ (Young forest) $p$ (.)	3	56	98.38	104.84	0.379	0.18
$\Psi$ (.) $p$ (.)	2	56	101.67	105.89	1.429	0.09
$\Psi$ (Forestry proximity) $p$ (.)	3	56	99.71	106.18	1.712	0.08
$\Psi$ (Coniferous forest) $p$ (Last snowfall)	4	56	97.96	106.74	2.277	0.07
$\Psi$ (Sample year) $p$ (.)	3	56	100.54	107.01	2.542	0.06
$\Psi$ (Young forest, Coniferous forest) $p$ (Last snowfall)	5	56	95.88	107.08	2.615	0.06
$\Psi$ (Young forest) $p$ (Last snowfall)	4	56	98.35	107.13	2.670	0.06
$\Psi$ (Snow condition) $p$ (.)	3	56	101.58	108.04	3.574	0.04
$\Psi$ (Road density) $p$ (.)	3	56	101.65	108.12	3.653	0.03
$\Psi$ (Road density, Forestry proximity) $p$ (.)	4	56	99.71	108.5	4.033	0.03
$\Psi$ (Young forest, Coniferous forest, Road density, Forestry proximity, Snow condition, Sample year) $p$ (Last snowfall)	9	56	94.16	116.08	11.614	0

Variables predicted to influence the probability of species occurrence are preceded with ( $\Psi$ ) and factors predicted to influence the detection probability are preceded with ( $p$ ). Models where probabilities of occurrence ( $\Psi$ ) or detection probability ( $p$ ) are assumed constant are denoted by a period,  $\Psi$  (.) or  $p$  (.) respectively

**Table 4** Parameter estimates for a composite model of Canada lynx (*Lynx canadensis*) occurrence in central Ontario, Canada, including standard error (SE), 95% confidence intervals, and importance value of the model averaged variable

	Estimate	SE	95% CI		Importance Value
			Upper	Lower	
Site intercept estimate	-1.69	0.44	-0.9421	-2.4280	-
Young forest estimate	1.92	1.07	3.7211	0.1229	0.3510
Coniferous forest estimate	2.33	1.18	4.3145	0.3536	0.3582

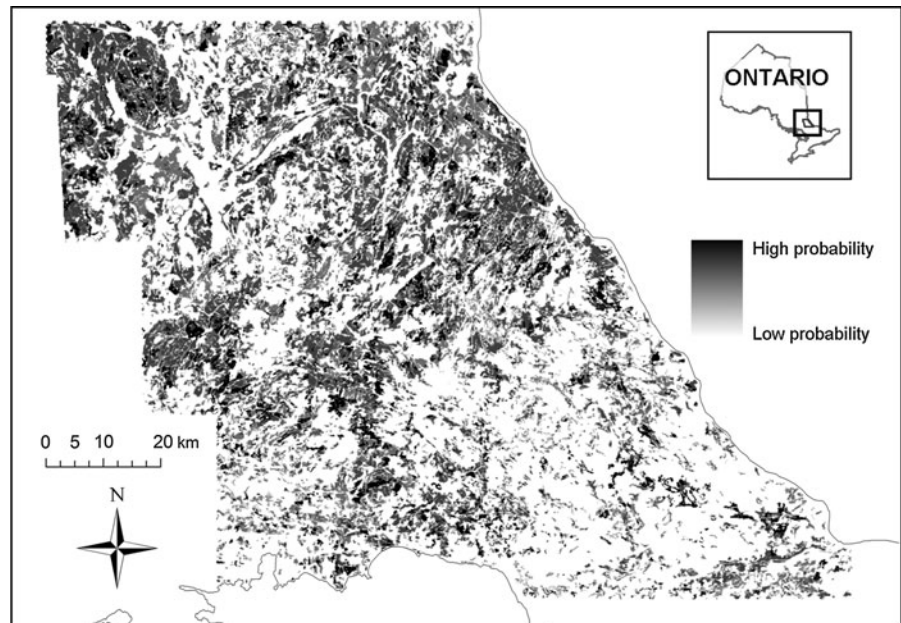
extended into the southern portion of the study area (Fig. 4). Mean (SE) length of backtracked lynx trails was 1,667 (79) m (range = 416–2,198 m). There was no correlation between explanatory variables used in modeling and the length of back tracked lynx trails (all  $p > 0.05$ ). The mean (SE) length of simulated random paths was 1,651 (3) m (range = 1,555–1,735 m). Lynx paths traveled through cells with significantly higher current than random paths (Mann–Whitney U test;  $Z = -4.077$ ,  $p < 0.0001$ ; Fig. 3B), suggesting both that the landscape was functionally connected for lynx in our study area, and that lynx selected connected routes to travel.

## Discussion

Lynx occurrence in the study area was best predicted by young coniferous forest. Our averaged model suggested that both young and coniferous forest had a positive and roughly equal effect on probability of lynx occurrence. Lynx habitat use during the winter period appears driven by the availability of their primary prey, snowshoe hare (Poole 2003). Selection of young coniferous forests by lynx in our study is consistent with previous findings (e.g., Murray et al. 1994; Mowat et al. 2000; Vashon et al. 2008b) and closely reflects habitat preference of snowshoe hare



**Fig. 2** Probability of Canada lynx (*Lynx canadensis*) occurrence throughout a study area in central Ontario, Canada. Probability is based on the prevalence of young coniferous forest in 0.0225 km<sup>2</sup> pixels (150 m × 150 m)



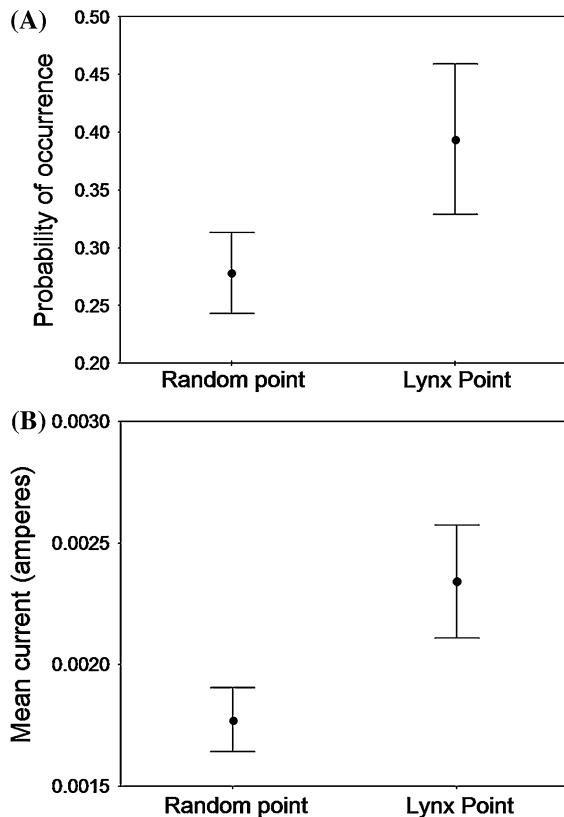
(Murray 2003; Fuller et al. 2007). Lynx are known to select habitat based on hare abundance in the core of the occupied lynx range (Murray et al. 1994). The validation of our connectivity model suggests that lynx will also select hare habitat while moving along the range periphery, and thus, that young coniferous forest contributes to functional connectivity for peripheral lynx populations. Our study also demonstrated that lynx selected habitats that were connected. This implies that habitat configuration may be an important element of functional connectivity for lynx, and an important conservation consideration for lynx on the range periphery.

Lynx are a wide-ranging species (Burdett et al. 2007) and lynx densities along the periphery are generally low due to the patchy distribution and sparse nature of suitable habitat relative to the core (Guo et al. 2005). These two factors led to low occupancy rates and few detections at the samples sites. However, despite our small sample size of occurrences, our models included information from both detection and non-detection locations. This fact, in addition to the specialized nature of lynx habitat use, permitted the development of a robust yet simple model of occurrence that was supported by an independent data set of lynx observations.

We have no accurate data on lynx population sizes in the region. However, extrapolating the density

estimate of 4.5 adult lynx per 100 km<sup>2</sup> from a nearby jurisdiction (Vashon et al. 2008a) suggests there may have been about 180 adult lynx in our 4,000 km<sup>2</sup> study area, assuming saturation. Our models suggest that the area was not saturated, and thus that there were <180 lynx. Nevertheless, the size of our study area and the scale of lynx movement both imply that we sampled numerous individuals. Our modeling indicated a greater probability of occurrence and more contiguous lynx habitat in the north compared to the south, which likely also corresponded to a gradient in lynx density. These findings are consistent with previous studies that suggest a negative relationship between lynx densities and distance from the range core (Schwartz et al. 2002; Bayne et al. 2008). Peripheral lynx populations are thought to expand and contract with pulsed dispersal from the range core, depending on hare density (O'Donoghue et al. 2010), but longer term trends of lynx populations on the southern range periphery have been a northward contraction (Laliberte and Ripple 2004).

Forest management was ongoing throughout the study region; we failed however, to detect an effect of this variable on lynx occurrence (Table 3). Our forest management variable addressed recent forestry activities (<5 years) whereas older cuts were classified by development stage and forest type. Previous studies have found that lynx occurrence is negatively



**Fig. 3** Comparison of (A) occurrence probabilities underlying point locations of Canada lynx (*Lynx canadensis*) detected (mean = 0.394,  $n = 38$ ) independently of model creation data and pseudo-absence points (mean = 0.278,  $n = 120$ ) and (B) mean current values underlying backtracked lynx trails (mean = 0.00234 amperes,  $n = 31$ ; Mann–Whitney U test;  $Z = -3.491$ ,  $p = 0.0005$ ) and simulated random paths (mean = 0.00177 amperes,  $n = 100$ ; Mann–Whitney U test;  $Z = -4.077$ ,  $p < 0.0001$ ) within 4 km of surveyed roads and trails. High current values represent areas with high net movement probability of random walkers and highlight potential north–south corridors along the southern periphery of the lynx range in Ontario

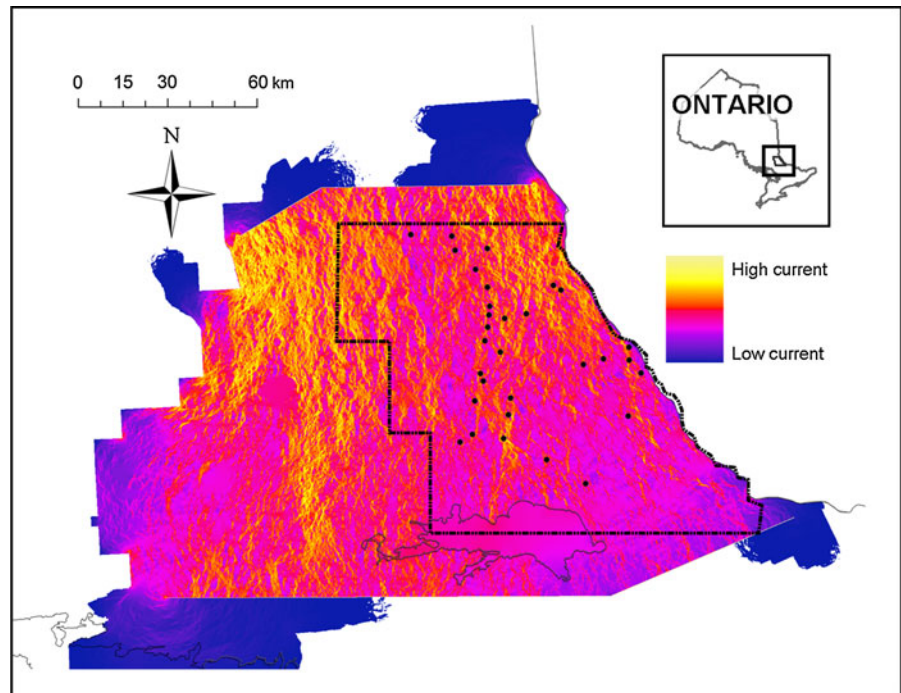
correlated with recent cuts but positively correlated with older clear cuts (Hoving et al. 2004). It seems likely that our results echo similar relationships but from a forest stand composition and development stage perspective rather than a forest management one. This also implies that forest succession will play a role in the amount and availability of suitable lynx habitat as well as functional connectivity along the periphery (see Vashon et al. 2008b). Although roads have been known to influence the occurrence of lynx in other studies, proximity to roads appeared not to affect lynx space use in our study area. Indeed, we detected no

relationship between the proximity of transects to roads, the other explanatory variables or lynx occurrences. Further, lynx movement behaviour did not vary with distance from the road. These findings suggest that roads did not influence lynx occurrence or movement in our study area. The narrow width and low vehicle traffic volume that we observed during winter may not represent a sufficient barrier or deterrent to lynx in central Ontario. We also found no effect of snow on lynx occurrence and attribute this to the relatively small spatial scale over which our study took place, resulting in lower variability in snowfall compared to other larger scale studies where lynx occurrence was influenced by snow (e.g., Hoving et al. 2005).

We considered a year effect in our model because we were concerned that interannual changes in snow depth or lynx abundance would influence patterns of lynx occurrence between years. However, we detected no influence of snow condition or year on the probability of lynx occurrence. Thus, despite the few transects visited in the second year of the study and the significant change in snow depth, we detected no influence of these variables on our model of lynx occurrence.

Occupancy models make the assumption that survey sites experience a constant state of occupancy throughout the sampling season (i.e., the closure assumption; Rota et al. 2009). This assumption is often difficult to meet for large wide-ranging species. Ideally, the sample site area would be equal in size to the home range of the target species. Home range sizes of lynx vary substantially through time, space and between sexes, with male home ranges usually being larger than those of females (Vashon et al. 2008a). Moreover, home range size is larger for lynx in peripheral populations and during the low phase in the cycle of hare abundance compared to lynx in the core of the range and during the peak hare densities (Poole 2003). Generally, lynx have home ranges up to and exceeding 50 km<sup>2</sup> along the southern range periphery (Poole 2003; Vashon et al. 2008a). Of course, conducting repeated and thorough surveys over an area this large is logistically impractical. Even if it was practical to survey such an area, it would be nearly impossible to ensure that the sample site did not overlap a home range edge and thus violate the assumption of a constant state of site occupancy. In situations such as these and assuming that changes

**Fig. 4** Map of simulated electric currents identifying functional connectivity through Canada lynx (*Lynx canadensis*) habitat from nodes to the north and south of the study area in central Ontario, Canada. Black points depict the origins of backtracked lynx trails ( $n = 31$ ) that were used to validate the current map



in site occupancy occur at random, ‘occupancy’ can instead be interpreted as ‘use’ (Mackenzie 2005). Although this violation of the closure assumption to some degree alters the interpretation of occupancy, it does not bias patterns of connectivity or habitat use predicted by our models (Kendall 1999).

Our study represents a novel approach to the parameterization of landscape resistance surfaces (e.g., Spear et al. 2010). We developed an occupancy model from repeated snow track surveys at random sites to estimate the probability of lynx occurrence and applied the model to derive a resistance surface, thereby linking occupancy models with functional connectivity. Our approach assumes that probabilities of occurrence are indicative of landscape resistance to movement. Essentially, we assumed that patterns of lynx movement between patches in the landscape were governed by the intervening quality of habitat (McRae et al. 2008), and that all different types of movement behaviors were similar in this regard. If these assumptions were incorrect, for example, if lynx did not select habitat while dispersing, then both the accuracy and precision of our model would be reduced. Our model validation supported the assumed relationship between movement and occupancy however, revealing that, indeed, lynx traveled through

landscapes with higher current than random. Thus, high current density represented high lynx movement probability, where movement likely included a variety of different behaviours, including natal and environmental dispersal,

Movement corridors are frequently viewed simplistically, as small-scale, linear habitats that facilitate movement between disconnected patches embedded in an unsuitable matrix (Cushman et al. 2009). Corridors may be more realistically considered in many landscapes as a heterogeneous cost surface (Cushman et al. 2009), and this appears to be the case for lynx at their southern range periphery. Cyclic lynx populations produce synchronized pulses of dispersing lynx from the range core that are assumed to supplement sink populations in peripheral landscapes (Schwartz et al. 2002; Murray et al. 2008). Our modeling identified several long and wide corridors connecting northern core landscapes to peripheral lynx habitats through a landscape characterized by a continuum of habitat quality and movement probabilities and these connective landscapes were used by lynx for movement. Maintaining habitats that connect sink populations with the core is important for ensuring long-term persistence of peripheral populations dependent on immigration. Indeed, peripheral

populations in general are relevant to conservation because they carry adaptive potential that can guide future speciation events (Lesica and Allendorf 1995).

Our study demonstrated a novel approach for identifying connective habitats along a species' range periphery by employing an empirical occupancy model combined with circuit theory to predict corridors through a relatively intact and unfragmented heterogeneous landscape. The conservation of existing corridors may be the most effective means of maintaining functional connectivity since existing natural corridors are most likely to be used by dispersing animals (Gilbert-Norton et al. 2010). The techniques described herein are of potential use for conservation of species or for systems requiring objective knowledge of habitats that increase functional connectivity between small and isolated populations. We suggest that our method can be used for assessing similar threats of isolation and numeric decline in populations occupying marginal habitat.

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