Habitat Loss, Not Fragmentation, Drives Occurrence Patterns of Canada Lynx at the Southern Range Periphery

Megan L. Hornseth¹*, Aaron A. Walpole², Lyle R. Walton³, Jeff Bowman², Justina C. Ray⁴, Marie-Josée Fortin⁵, Dennis L. Murray⁶

Abstract

Peripheral populations often experience more extreme environmental conditions than those in the centre of a species’ range. Such extreme conditions include habitat loss, defined as a reduction in the amount of suitable habitat, as well as habitat fragmentation, which involves the breaking apart of habitat independent of habitat loss. The ‘threshold hypothesis’ predicts that organisms will be more affected by habitat fragmentation when the amount of habitat on the landscape is scarce (i.e., less than 30%) than when habitat is abundant, implying that habitat fragmentation may compound habitat loss through changes in patch size and configuration. Alternatively, the ‘flexibility hypothesis’ predicts that individuals may respond to increased habitat disturbance by altering their selection patterns and thereby reducing sensitivity to habitat loss and fragmentation. While the range of Canada lynx (Lynx canadensis) has contracted during recent decades, the relative importance of habitat loss and habitat fragmentation on this phenomenon is poorly understood. We used a habitat suitability model for lynx to identify suitable land cover in Ontario, and compared occupancy patterns across landscapes differing in cover, to test the ‘threshold hypothesis’ and ‘flexibility hypothesis’. When suitable land cover was widely available, lynx avoided areas with less than 30% habitat and were unaffected by habitat fragmentation. However, on landscapes with minimal suitable land cover, lynx occurrence was not related to either habitat loss or habitat fragmentation, indicating support for the ‘flexibility hypothesis’. We conclude that lynx are broadly affected by habitat loss, and not specifically by habitat fragmentation, although occurrence patterns are flexible and dependent on landscape condition. We suggest that lynx may alter their habitat selection patterns depending on local conditions, thereby reducing their sensitivity to anthropogenically-driven habitat alteration.

Introduction

Populations occurring at the periphery of a species’ geographic range often occupy habitats that are of lower overall quality, leading to reduced survival, reproduction and population density, compared to populations in the core of the range [1]. In addition, peripheral populations tend to be more sensitive to environmental variability than those in the core, which can promote increased demographic stochasticity and lower resilience [2–4]. As a result, individuals in the range periphery may be more sensitive to the processes of habitat loss and fragmentation. Alternatively, animals may respond with more flexible habitat selection patterns, enabling them to move among variable environments to enhance their fitness [5]. This flexibility should increase species’ persistence in landscapes experiencing anthropogenic change, such as in areas subject to high fragmentation. However, much of our perception of how wide-ranging species respond to these landscape-scale processes is speculative, especially in peripheral populations where both occurrences and their detection probability are often limited. This shortcoming is especially relevant because as landscapes continue to be altered by anthropogenic disturbance, many species are faced with declines in range size [6]. An improved understanding of the effects of habitat loss and fragmentation on species occurrence patterns will enhance our understanding of how these processes may impact species distributions.

Habitat loss and fragmentation are separate processes whereby habitat loss is an overall reduction in the amount of suitable habitat resulting in a decline in patch size and habitat fragmentation is the breaking apart of habitat, independent of habitat loss [7]. While the effects of habitat loss on species are consistently negative, the effects of habitat fragmentation are less well understood, as few studies measure fragmentation independently of habitat loss [7]. While
Habitat fragmentation can have both weakly positive and weakly negative effects on biodiversity and population size, the impact of these effects is often far less important than the effects of habitat loss [7–9]. There is some evidence that the effects of habitat fragmentation depend upon the amount of habitat that is available in a landscape. The ‘threshold hypothesis’ predicts that individuals will be more affected by habitat fragmentation when the amount of habitat on the landscape is limiting (i.e. less than 30% habitat); and small and isolated patches become more numerous, than when habitat is abundant and patches are larger and more continuous [10,11]. Habitat fragmentation may compound the effects of habitat loss due to changes in patch size and landscape configuration, implying that fragmentation may have a greater effect at the range periphery, where habitat is often limiting [2]. This hypothesis has been supported by several studies examining population size and presence of birds and small mammals with habitat thresholds ranging from 10–30% [10,12–14]. In contrast, the ‘flexibility hypothesis’ suggests that individuals may alter their habitat selection patterns, permitting them to inhabit variable environments that would otherwise be unsuitable due to habitat fragmentation [5,15].

Canada lynx (Lynx canadensis) occur across the boreal forest of North America, where their primary prey is snowshoe hare (Lepus americanus). Since lynx are dependent upon snowshoe hares, they select forested habitat based on high hare abundance or where they are most easily depredated [16–18], whereas hares select young coniferous forests where both food and cover are adequate [19,20]. In the southern periphery of the lynx range, forest composition is more heterogeneous and hare densities are naturally lower, leading to reduced abundance and restricted distribution of lynx [21], which require densities between 1 to 1.5 hares per hectare to persist [22]. Because habitat for both lynx and hare has become both reduced and fragmented due to anthropogenic activities in their southern ranges, the distribution and abundance of both species is now restricted [23,24]. This has reduced genetic diversity in southern populations of both hare [25] and lynx [26]. Additionally, the southern range of lynx in Ontario has contracted by over 175 km since 1970 [26]. Although the mechanisms ultimately limiting lynx populations at the southern range periphery remain to be fully understood, this may be due to sensitivity to habitat fragmentation [27], with habitat loss and climate change as other important factors [26]. Several other felid species are also reported to be sensitive to habitat fragmentation (e.g. Iberian lynx (Lynx pardinus) [28], bobcat (Lynx rufus) and cougar (Puma concolor) [29]). However, whether these species express any flexibility in selection patterns in relation to the amount of habitat on a landscape or whether these patterns hold true for habitat fragmentation, has not yet been explored.

We examined the occurrence patterns of Canada lynx across the 2 regions in the southern geographic range of the species in Ontario to assess patterns of occurrence in relation to habitat loss and fragmentation. Given that lynx are prey specialists, requiring areas within a narrow range of suitable conditions to meet prey and habitat requirements [30] as well as connectivity requirements [31], we predicted that lynx would be sensitive to habitat loss when habitat was widely available, and sensitive to both habitat loss and fragmentation when suitable habitat was less than 30%; this would support the ‘threshold hypothesis’ [10,11]. These patterns may be expressed more strongly near the southern range periphery, due to increased levels of habitat loss and reduced habitat quality [26], leading us to speculate that any sensitivity to habitat fragmentation would be most apparent there. Alternatively, the ‘flexibility hypothesis’ suggests that lynx will have tolerance to both habitat loss and fragmentation, such that their occurrence patterns may not correlate with either process, indicating flexibility in habitat selection. We developed a habitat suitability model for lynx and tested the above predictions using patterns of track occurrence across the species’ southern range periphery. We compared two regions each with three similar levels of suitable land cover as determined by the habitat suitability model, to examine if occurrence patterns differ across landscapes with varying amounts of suitable land cover. Observations of lynx tracks in areas with limited suitable land cover and increased fragmentation would imply that lynx are not sensitive to habitat fragmentation, or that the importance of suitable habitat on occurrence patterns at the range periphery are less critical than previously understood.

Methods

Ethics Statement

The Trent University Research Ethics Board approved the study (reference #21083). In the introduction of the study, participants were explicitly told that informed consent was implied if they submitted their survey data. The field component consisted of non-invasive track surveys conducted on public land, so no access permits or animal care protocols were required. Canada lynx are considered not at risk under provincial and federal guidelines.

Study Area

The study area encompassed 200 000 km² in central Ontario (Figure 1A), across the southern boreal forest and the Great Lakes St. Lawrence forest, a transition zone from boreal to deciduous forest, encompassing the southern range limit of lynx occurrence in the region [32]. The area is largely comprised of boreal forest, with spruce (Picea glauca, P. mariana), balsam fir (Abies balsamea), trembling poplar (Populus tremuloides) and white birch (Betula papyrifera) as dominant tree species. The southerly portions of the study area in the Great Lakes St. Lawrence region include pines (Pinus resinosa, P. strobus), eastern hemlock (Tsuga canadensis), yellow birch (B. alleghaniensis) and maples (Acer saccharum, A. rubrum). Habitat loss and fragmentation throughout the study area is caused primarily by forestry and associated road construction. Historically 1% of the entire region (approximately 2000 km²) was harvested annually [32], current levels are 0.04% or 800 km² (2000–2010 average; [33]). Other sources of habitat loss include populated areas, agriculture, and natural disturbance such as forest fire and pest infestations.

Habitat Suitability Model

In order to quantify lynx habitat suitability, we used the analytic hierarchy process, a decision-making procedure that is useful in the development of habitat suitability models for wide-ranging mammals (see [34,35] for description of methodology). We developed the survey design based on a literature review identifying important ecological factors affecting lynx occurrence, with an emphasis on the southern range periphery. The primary habitat characteristics were land cover attributes (e.g., [17,18]), forest age class (e.g., [18,36]), annual snowfall (e.g., [37]) and road density (e.g., [38]). We developed two separate models of habitat suitability, one based on expert-opinion, where we received 11 solicited responses from lynx researchers across North America, and the other using a literature-based approach with four ‘naïve’ participants with no previous knowledge of lynx ecology. Both experts and naïve participants received the same survey and the naïve participants also received four research papers providing a detailed description of the basic habitat requirements of lynx from across its range [17,18,38,39]. The survey consisted of five
separate pair-wise comparison matrices based on each of the features of interest (land cover, forest development stage, snowfall, and road density) and an overall comparison of the relative importance among all features. The overall ranking of features was used to weight parameters within the model and estimate the relative importance of factors affecting lynx habitat suitability, whereas weights within a feature determined the ranking for its attributes.

We used the Ontario Forest Resource Inventory to characterize land cover; these data provide a detailed description of species composition and forest stand age as determined by aerial photo interpretation. The study area included 41 provincial forest management units, and each unit was updated with forest fire and harvest information up to and including 2008. Standardized forest units were combined to create six generalized land cover types (coniferous forest, deciduous forest, mixedwood forest, developed land, wetland, and open areas) and five forest development stages (presapling, sapling, immature, mature and old; [40]), which improved the accuracy of the dataset [41]. We converted the land cover map to a geospatial raster for analysis; all GIS analyses were conducted in ArcGIS 9.2 (ESRI, Redlands, CA, USA).

We evaluated the lynx habitat model in a portion of the study area near the North Bay - Temagami region of northeastern Ontario, Canada (47.01°N, 79.97°W; see Figure 1A). The Temagami region is approximately 8,000 km² and was selected...
because it is located within the southern range periphery of lynx in Ontario and the transition zone of boreal forest with the northern Great Lakes-St. Lawrence forest. Between January and March 2009, we surveyed lynx occurrence at 40 randomly selected sites that represented a gradient in available land cover types [38]. We assessed lynx presence by snowtracking triangular transects around the centroid of the cell (dimensions 0.5 km per side, [38]). Additional lynx tracks that were encountered opportunistically while travelling within the landscape were also considered as lynx presence. We calculated habitat suitability at the centre of each transect and each opportunistic track, using both models. We used receiver operating characteristic plots and the Area Under the Curve (AUC) as an independent measure of model accuracy via the program ROC/AUC [42]. AUC provides a measure of model accuracy, where values >0.7 indicate good model fit. We selected $P_{\text{f}}}i_{\text{art}}$, the value where specificity and sensitivity are equal, as the threshold habitat suitable for lynx occurrence.

Lynx Occurrence Sampling

Two regions were selected to document lynx occurrence (estimated by track identification) in landscapes across a gradient of habitat fragmentation. Each region fell within the larger study area which encompassed the southern boreal forest and Great Lakes-St. Lawrence Forest, and was divided into three landscapes based on the amount of suitable land cover (high, moderate, and low) as determined by the habitat suitability model (Figure 1B). The Chapleau region was 12 900 km$^2$, located primarily in the boreal forest. The western portion of the region had the highest amount of suitable land cover and is the least fragmented landscape in this region. The central area of the Chapleau region is highly fragmented with the most habitat loss due to forestry, roads, and human settlements. The easternmost portion of this region has a moderate amount of suitable land cover and a moderate level of fragmentation due to forestry roads (Table 1). The Mississagi region was 12 800 km$^2$, located primarily in the Great Lakes St. Lawrence forest. The northern portion of this region had moderate amounts of suitable land cover, but was fragmented due to forestry roads; the central portion had the highest amount of suitable land cover and was least fragmented, and the southernmost landscape had the least amount of suitable land cover in this region, with habitat loss due to forestry, human settlements and roads. These regions were surveyed for occurrence of lynx tracks from January to March 2010 and each identified track point was recorded as a lynx occurrence. All forest access roads, trails, hydro-electric line corridors, cutovers and riparian areas were sampled via snowmobile, totalling 9 320 km of survey lines in both landscapes. All lynx track locations were documented; the centroid of the cell (dimensions 0.5 km per side, [38]). Additional lynx tracks that were encountered opportunistically while travelling within the landscape were also considered as lynx presence. We calculated habitat suitability at the centre of each transect and each opportunistic track, using both models. We used receiver operating characteristic plots and the Area Under the Curve (AUC) as an independent measure of model accuracy via the program ROC/AUC [42]. AUC provides a measure of model accuracy, where values >0.7 indicate good model fit. We selected $P_{\text{f}}}i_{\text{art}}$, the value where specificity and sensitivity are equal, as the threshold habitat suitable for lynx occurrence.

Habitat Loss Drives Occurrence Patterns of Canada Lynx

We used PatchMorph [44] and the habitat suitability model to estimate a ‘functionally’ connected landscape for lynx from: (1) a critical threshold of habitat suitability value of 52, (2) a minimum patch size of 5 ha (the minimum mappable forest stand [Ontario Ministry of Natural Resources, unpublished data]), and (3) a crossing distance of 200 m (M. Hornseth, unpublished data). Note that crossing distance is defined as the distance that lynx will travel in unsuitable habitat; the minimum for this metric is two raster pixels and parameters were set conservatively as per published observations of lynx habitat use patterns (see [17,45]). Although we acknowledge that actual functional connectivity requirements for lynx are just beginning to be understood (see [46]), we consider our selected values as being within the range of those that are plausible, with minor deviations likely affecting our results only qualitatively. Additionally, we did a sensitivity analysis with crossing distances of 200 to 1000 m in 400 m increments to determine the effect of this parameter on our estimates of connectivity.

Effective mesh size can be defined as the average area potentially accessed by an animal on a given landscape without having to cross defined borders or low quality habitat, so larger values indicate that the landscape is more connected and smaller values indicate the landscape is more fragmented [44,47]. We used effective mesh size ($M_{\text{eff}}$) as our measure of habitat fragmentation in ArcMap 10.1 [48]. $M_{\text{eff}}$ is calculated by:

$$M_{\text{eff}} = \frac{1}{A_{\text{e}}} \sum_{i=1}^{n} A_{i}^2,$$

where $A$ is the area of a single patch and $A_{\text{e}}$ can be either the total area of the polygon or the total amount of suitable habitat (i.e., the sum of all patch areas). In order to remove correlation between habitat amount and effective mesh size, we used the total amount of suitable habitat as the denominator (L. Fahrig, pers. comm.). Since correlations were still high (0.63–0.86), we regressed $M_{\text{eff}}$
against habitat amount and used the residuals as our estimate of habitat fragmentation ($\text{M}_{\text{eff}}$).

**Data Analysis**

We aimed to determine whether lynx are limited by habitat amount, fragmentation, or both processes, by contrasting patterns on landscapes with different amounts of suitable land cover. We hypothesized that lynx habitat requirements would restrict their occurrence to highly-connected areas in each landscape. We used one-sided unpaired t-tests to examine whether habitat amount and fragmentation were greater in presence areas than pseudo-absence areas at each spatial scale among landscapes with high, moderate, and low amounts of habitat amount in each region. We examined any correlations between these two within each region and landscape.

We tested 3 a priori hypotheses to explain lynx occurrence: i) lynx occurrence is limited only by fragmentation, ii) lynx occurrence is limited only by habitat loss, and iii) lynx occurrence is limited by both habitat amount and fragmentation. We used logistic regression and standard model selection procedures to determine which hypothesis best explained lynx occurrence in landscapes across the levels of suitable land cover. We used Akaike’s information criterion to evaluate the candidate models for each lynx and pseudo-absence area and landscape within each region. We considered $\Delta$AIC > 2 to indicate a significant difference in model likelihood [49]. AIC does not assess model performance, and only models that performed well were considered plausible for the AIC model selection, so we used the Logistic Regression $\chi^2$ model likelihood ratio test to determine model fit.

**Results**

**Habitat Suitability Model**

Both the expert-opinion and literature-based models suggested that coniferous forest land cover, and forest in a sapling developmental stage, provided the most suitable habitat for lynx. However, models differed with respect to the relative importance of overall features, with the literature-based model suggesting that land cover was only slightly (1.04 times) more important than development stage whereas expert opinion suggesting that development stage was substantially (1.20 times) more important than land cover type. We omitted annual snowfall and road density from the final habitat suitability models due to low overall importance in both models (see Table S1 in Information S1).

We detected lynx at 19% ($n = 48$) of the sites within the Temagami landscape; we also included 14 more lynx track occurrences that we encountered opportunistically within the study site, increasing the total number of validation locations to 62. The literature-based model had a good overall fit (AUC: 0.912, $p<0.001$) and correctly predicted 83.9% of all sites ($n = 62$) and 82.6% of lynx occurrences ($n = 23$). The expert opinion model had a comparable fit (AUC: 0.855, $p<0.001$), correctly classifying 82.3% of all sites and 78.2% of lynx occurrences. Although both models performed well, the literature-based model surpassed the expert-opinion model in every comparison (see Table S1 in Information S1) and was selected for the remaining analyses (see Table S2 in Information S1).

**Landscape Characteristics**

The landscapes within both regions had similar amounts of suitable land cover (Table 1), but different levels of habitat fragmentation. The high-cover landscape in Chapleau consisted of 41.9% suitable land cover with an effective mesh size of 87.3 km$^2$. In Mississagi, the high-cover landscape had approximately the same amount of suitable land cover (42.8%), but a much larger mesh size of 258.6 km$^2$. The landscapes with a moderate amount of suitable land cover in the Chapleau and Mississagi regions had similar amounts of suitable land cover (35.0% and 31.9%, respectively) and mesh sizes (22.4 km$^2$ and 23.1 km$^2$, respectively). The low-cover landscapes had similar amounts of suitable land cover (20.6% in Chapleau, and 25.5% in Mississagi), however, the landscape in the Chapleau region was substantially more fragmented ($\text{M}_{\text{eff}}$ 5.7 km$^2$) in comparison to the matched landscape in the Mississagi region ($\text{M}_{\text{eff}}$ 18.6 km$^2$). This indicated that although the two landscapes had similar amounts of suitable land cover, generally the Chapleau landscape was more fragmented.

**Lynx Occurrence**

Where possible, lynx selected areas with higher amounts of high quality habitat (structural connectivity) at the 25 km$^2$ spatial scale (Table 2). There was a positive correlation between the amount of suitable habitat and lynx occurrence areas in each high- and moderate-levels of suitable land cover in the Chapleau region, and in the landscape with a moderate-level of suitable land cover in the Mississagi region at the 25 km$^2$ area (Figure 2). In both regions, on landscapes with high- and moderate-levels of land cover, lynx consistently occurred in areas with at least 50% habitat and avoided areas with <30% habitat (Figure 3). However, in the low-cover landscapes, approximately half of lynx occurrences had less than 30% habitat at a spatial scale of 25 km$^2$. These trends were consistent across both regions. At a spatial scale of 100 km$^2$, there were no correlations between the amount of suitable habitat and lynx occurrence at any level of suitable land cover (Table 3). Once
Table 2. Summary of the differences in connectivity measures of Canada lynx occurrence and pseudo-absences in Ontario, Canada: all t-tests were one-sided with p-values <0.05 in bold and p-values <0.1 in italics.

| Region     | Area (km²) | Land Cover Level | Variable | Present | Pseudo-absent | t-test | p-value |
|------------|------------|------------------|----------|---------|---------------|--------|---------|
| Mississagi | 25         | High             | Habitat² | 56.56   | 54.90         | 0.53   | 0.300   |
|            |            |                  | Meff²    | 0.17    | -0.20         | 0.76   | 0.223   |
|            |            | Moderate         | Habitat  | 48.18   | 33.8          | 3.55   | <0.001  |
|            |            |                  | Meff²    | 0.17    | -0.20         | 0.76   | 0.223   |
|            |            | Low              | Habitat  | 26.4    | 29.98         | -0.76  | 0.772   |
|            |            |                  | Meff residuals | -0.16 | 0.06 | -0.51 | 0.691 |
| 100        | High       | Habitat          | 47.98    | 47.72   | 0.10          | 0.461  |         |
|            |            |                  | Meff²    | -0.08   | 0.09         | -0.26  | 0.601   |
|            |            | Moderate         | Habitat  | 35.35   | 31.11         | 1.33   | 0.095   |
|            |            |                  | Meff²    | 1.12    | 0.66         | -1.92  | 0.970   |
|            |            | Low              | Habitat  | 23.22   | 27.64         | -0.97  | 0.829   |
|            |            |                  | Meff²    | -0.24   | 0.10         | -0.43  | 0.665   |
| Chapeleau  | 25         | High             | Habitat  | 52.79   | 46.39         | 1.96   | 0.027   |
|            |            |                  | Meff²    | 0.27    | 0.18         | -0.76  | 0.774   |
|            |            | Moderate         | Habitat  | 51.88   | 43.31         | 3.01   | 0.002   |
|            |            |                  | Meff²    | 0.36    | 0.44         | -1.98  | 0.975   |
| 100        | High       | Habitat          | 29.87    | 29.88   | -0.01         | 0.502  |         |
|            |            |                  | Meff²    | 0.04    | -0.03        | 0.31   | 0.380   |
|            | Low        | Habitat          | 41.16    | 39.88   | 0.52          | 0.300  |         |
|            |            |                  | Meff²    | -0.74   | 0.51         | -1.29  | 0.899   |
|            |            | Moderate         | Habitat  | 39.78   | 34.75         | 2.33   | 0.011   |
|            |            |                  | Meff²    | 0.41    | 0.50         | -1.30  | 0.901   |
|            |            | Low              | Habitat  | 22.22   | 21.89         | 0.14   | 0.442   |
|            |            |                  | Meff²    | -0.12   | 0.07         | -0.96  | 0.829   |

Land cover is the amount of suitable land cover measured at the landscape level as determined by the habitat suitability model.

Habitat is the proportion of suitable habitat within each lynx- and pseudo-absence area based on the habitat suitability model.

Meff² is the residual of habitat regressed against mesh size (km²; see text), a measure of functional connectivity, within each lynx- and pseudo-absence area.

doi:10.1371/journal.pone.0113511.t002
the effect of habitat amount was removed, there was no correlation between habitat fragmentation \( M_{\text{dif}} \) and lynx occurrence on any landscape, at either spatial scale (Table 2).

Lynx occurrence patterns differed across landscapes, but the trends were consistent across regions. In the landscapes with moderate levels of suitable land cover, the top model included both the proportion of suitable habitat and habitat fragmentation lynx occurrence. However, only the proportion of suitable habitat had a positive association on lynx occurrence, \( M_{\text{dif}} \) had a negative correlation with lynx occurrence indicating that lynx selected areas with higher amounts of fragmentation (Figure 4; Table 3). In the high- and low-cover landscapes in both regions, there was no significant correlation between lynx occurrence patterns and proportion of suitable habitat or effective mesh size (Table 3).

Sensitivity Analysis

We examined 3 crossing distances in the PatchMorph output to determine if crossing distance was either underestimated or strongly influential on lynx occurrence. We tested crossing distances of 200 m, 600 m, and 1000 m, and used standardized regression coefficients from single variable logistic regressions to determine the level of influence. Effective mesh size coefficient estimates ranged from \(-0.02\) to \(0.04\), with no visible trend; none of the coefficients were significant \((p\) values ranged from \(0.228\)–\(0.589\)). Increasing the estimated crossing distance did not affect model fit.

Discussion

Our results confirm that lynx are not sensitive to habitat fragmentation at low levels of suitable habitat, and also suggest that lynx display considerable flexibility in habitat selection patterns, supporting the 'flexibility hypothesis'. We showed that in landscapes with moderate and high amounts of suitable land cover (30–35% and >40%, respectively), lynx occurred in areas with at least 30% available habitat and largely avoided areas below that threshold, while being unaffected by habitat fragmentation. Although this finding is consistent with the 'threshold hypothesis', this hypothesis also predicts that lynx would be more sensitive to habitat fragmentation on landscapes where suitable land cover was low. However, our results showed that on landscapes where suitable land cover was limited (<30%), lynx did not select areas with concentrated habitat and lynx occurrence patterns were not well correlated with either either habitat amount or habitat fragmentation, instead supporting the 'flexibility hypothesis'. Overall, we detected a threshold at which lynx occurrence patterns changed, but instead of being more sensitive to habitat fragmentation at low levels of suitable habitat, lynx displayed more flexibility in habitat selection on these landscapes. This indicates that lynx habitat choice is complex and either involves factors beyond mere resource preference, or selection of different land cover types in these areas.

Patterns of Occurrence

As predicted by the literature-based habitat suitability model, lynx were most likely to occur in sapling-stage coniferous forest. These results are consistent with other literature on lynx habitat ecology [17,18] and also describes snowshoe hare habitat preferences [19,20]. Road density and annual snowfall were not important for describing lynx occurrence in Ontario. This finding contrasts with previous work (e.g., [37,38]) but is consistent with a companion occupancy model within our study area [46], suggesting that these factors differentially affect lynx occurrence across their range and may be threshold-dependent. We surmise that low variation in snowfall patterns and low abundance of major highways as well as low road density in our study site may have accounted for the disparate results. Lynx occurrence, as determined by snow tracks across the study area, also supported this model, signifying that our model is generally robust. We recommend the use of this habitat suitability model as a tool to evaluate future forest condition on resource availability for Canada lynx in Ontario.

Flexibility in Response to Habitat Loss

Our results suggest that when approximately 30–35% of the landscape consists of suitable land cover, there is a strong correlation between the amount of suitable habitat and lynx occurrence. While this trend was not significant at higher levels of land cover at a landscape scale, in landscapes with both high and moderate amounts of suitable land cover, lynx occurrence patterns suggest that lynx preferred areas with at least 50% suitable land cover. While lynx will occur in some areas with less than 50% available suitable land cover, lynx consistently avoided areas with less than 30% suitable habitat when suitable land cover was abundant at a landscape level. This is consistent with previous work on small mammals and birds showing that habitat occupancy dynamics are determined by species-specific tolerance thresholds [7,11,13].
When suitable land cover comprised only 20–25% of the landscape, our results showed that there was no correlation between lynx occurrence and habitat amount, indicating some flexibility in habitat requirements on these landscapes. In contrast, when suitable habitat was limited, lynx did not avoid areas with less than 30% land cover and were not associated with areas with more than 50% suitable habitat, despite the local availability of these areas. It is possible that when suitable habitat is scarce, lynx can survive provided that hares, or suitable alternate prey, remain available on the landscape. This speculation is supported by observations of resident snowshoe hares occupying small patches <10 ha in fragmented landscapes [50,51] and the ability of lynx to include alternate prey items when hares are limited [31,52]. This pattern of labile specialization has been recently documented in birds, where the most specialized species tend to generalize their habitat selection pattern following disturbance [33]. However, the results of our study contrast with previous work by Swihart et al. [5,50], who showed that some species have greater sensitivity to habitat change at range margins. This suggests that there is a wide range of responses to habitat alteration and that further work is necessary to clarify the impact of landscape change on lynx.

Habitat Fragmentation

Our results show that there is no correlation between lynx occurrence patterns and habitat fragmentation (Meff.r). Meff.r (mesh size) measures the connectivity of a landscape, independent of habitat loss, so a negative coefficient indicates a positive relationship with habitat fragmentation. Our results suggest that there is a weakly negative relationship with Meff.r at moderate levels of suitable land cover, which is the opposite of what we predicted. In addition, the results from our sensitivity analysis suggest that increasing crossing distance does not improve the measure of habitat fragmentation for lynx. While some studies have suggested that habitat fragmentation may only be important when habitat amount is below 30% [9–11], our results do not support this hypothesis. At low levels of suitable land cover there was no relationship between habitat fragmentation and lynx occurrence, which is consistent with studies showing that the effects of habitat loss are generally far greater than the effects of habitat fragmentation [7,11]. Our results concerning habitat loss and habitat fragmentation are especially applicable to forestry-dominated landscapes, where silvicultural practices can result in marked shifts in habitat features for a variety of species, including higher densities of prey species such as snowshoe hares [54]. Therefore, we recommend that planning decisions regarding lynx consider the amount of total available habitat, which should generally improve chances of population persistence, while also benefiting overall landscape structure and function. This point is especially relevant at the southern range periphery of lynx, where
Table 3. Model selection of 3 a priori hypotheses proposed to explain lynx occurrence patterns across 3 landscapes differing in the amount of suitable landscape-level land cover in 2 regions (Chapleau and Mississagi) within an area of 25 km² for each lynx track and pseudo-absence.

| Landscape | Coefficients | AIC | ΔAIC | Weight | p-value |
|-----------|--------------|-----|------|--------|---------|
| **Chapleau** | | | | | |
| High Land Cover | | | | | |
| Habitat Only | - | 0.031* | 107.2 | 0 | 0.57 | 3.61 | 0.057 |
| Habitat + Meff.r | -0.079 | 0.032 | 108.3 | 1 | 0.28 | 4.36 | 0.113 |
| Meff Only | -0.072 | - | 110.2 | 3 | 0.15 | 0.61 | 0.454 |
| Moderate Land Cover | | | | | |
| Habitat + Meff.r | -0.253* | 0.086* | 108.7 | 0 | 0.71 | 13.00 | 0.002 |
| Habitat Only | - | 0.053* | 110.8 | 2 | 0.26 | 8.85 | 0.003 |
| Meff Only | -0.244 | - | 115.7 | 6 | 0.03 | 3.98 | 0.049 |
| Low Land Cover | | | | | |
| Meff Only | 0.098 | - | 100.3 | 0 | 0.43 | 0.06 | 0.802 |
| Habitat Only | - | 0.0001 | 100.4 | 0.1 | 0.41 | 0.00 | 0.996 |
| Habitat + Meff.r | 0.098 | -0.0002 | 102.4 | 2 | 0.15 | 0.11 | 0.945 |
| **Mississagi** | | | | | |
| High Land Cover | | | | | |
| Meff Only | 0.056 | - | 166.6 | 0 | 0.47 | 0.79 | 0.150 |
| Habitat Only | - | 0.006 | 166.9 | 0.5 | 0.36 | 0.28 | 0.596 |
| Habitat + Meff.r | 0.056 | -0.006 | 168.4 | 2 | 0.17 | 0.87 | 0.329 |
| Moderate Land Cover | | | | | |
| Habitat + Meff.r | -0.388* | 0.073* | 63.6 | 0 | 0.87 | 17.50 | <0.001 |
| Habitat Only | - | 0.053* | 67.8 | 4 | 0.12 | 11.27 | 0.008 |
| Meff Only | -0.390* | - | 73.3 | 9.7 | 0.01 | 5.68 | 0.017 |
| Low Land Cover | | | | | |
| Meff Only | -0.203 | - | 49.6 | 0 | 0.47 | 0.36 | 0.356 |
| Habitat Only | - | -0.016 | 49.7 | 0.1 | 0.39 | 0.45 | 0.511 |
| Habitat + Meff.r | -0.234 | 0.004 | 51.6 | 2 | 0.14 | 0.86 | 0.651 |

Asterisk (*) indicates significant coefficients at p<0.05, *indicates significance at p<0.1.

*Meff is the residual of habitat regressed against mesh size (km²); see text, a measure of functional connectivity, within each lynx- and pseudo-absence area.

Meff is the proportion of suitable habitat within each lynx- and pseudo-absence area based on the habitat suitability model.

DOI: 10.1371/journal.pone.0113511.t003
habitat loss is contributing to the northward regression of the species’ distribution [26].

Conclusion
Our results highlight the importance of examining habitat fragmentation independently of habitat loss to isolate and understand the impacts of each process [7,8]. While previous research suggests that closely related species, such as bobcats and Iberian lynx, are sensitive to habitat fragmentation [28,29], our results show that habitat loss, not fragmentation, drives occurrence patterns for Canada lynx. The effects of habitat loss and fragmentation may be species-specific, so we recommend that this hypothesis be further evaluated in both specialist and generalist species to improve our understanding of the impacts of these wide-spread processes. This is especially necessary for carnivores, which are considered to be sensitive to both habitat loss and fragmentation [35]. Ultimately, as rates of habitat loss and fragmentation continue to increase on a global scale, this and additional research can improve conservation efforts by ensuring that recovery strategies focus on the appropriate management action.

Supporting Information
Information S1 Comparison of expert opinion and literature-based models. Table S1. Performance metrics for the expert-opinion and literature based habitat suitability models for Canada lynx occurrence in Ontario, Canada. Receiver operating characteristic was based on 62 presence/absence locations near Temagami, Ontario. Bold text indicates better model performance. Table S2. Expert-opinion and literature based model weights for all variables used in the development of the habitat suitability model for Canada lynx in Ontario, Canada. Models were based on a survey using the analytic hierarchy decision-making process to rate the importance of different variables. The expert-opinion model is based on the replies of nine lynx researchers; the literature based model is based on the responses of 4 unbiased observers after having reviewed four research papers on lynx habitat selection. Figure S1. Distribution of Canada lynx occurrence across three landscapes differing in the amount of suitable land cover as determined by a literature-based habitat suitability model in the (A) Chapleau and (B) Mississagi Regions.

Acknowledgments
We thank K. Downing, L. Fahrig, E. Koen, K. Middel, and B. Pond for valuable input and feedback. We also thank all those who participated in the expert-opinion and literature-based surveys. Also thanks to T. Copeland, N. Woodhouse, E. Smith, A. Wilson, D. Ballak, and many volunteers for field support.

Author Contributions
Conceived and designed the experiments: MLH LW DLM JR MJF JB. Performed the experiments: MLH AAW. Analyzed the data: MLH DLM. Contributed reagents/materials/analysis tools: MLH JB AAW LW DLM. Wrote the paper: MLH.

References
1. Lawton J (1993) Range, population abundance and conservation. Trends in Ecology and Evolution 8: 409–413.
2. Gaston KJ (2003) The Structure and Dynamics of Geographic Ranges. New York: Oxford University Press. 266 p.
3. Grant MC, Antonovics J (1978) Biology of ecologically marginal populations of Anthozanthum odoratum. I. Phenetics and dynamics. Evolution 32: 822–838.
4. Yackulic CB, Sanderson EW, Uriarte M (2011) Anthropogenic and environmental drivers of modern range loss in large mammals. Proceedings of the National Academy of Sciences of the United States of America 108: 4024–4029.
5. Holt RD, Barfield M (2000) Habitat selection and niche conservatism. Israel Journal of Ecology and Evolution 54: 295–309.
6. Channell R, Lonolino MV (2000) Dynamic biogeography and conservation of endangered species. Nature 403: 84–86.
7. Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487–515.
8. Fahrig L (2002) Relative Effects of Habitat Loss and Fragmentation on Population Extinction. Journal of Wildlife Management 61: 603–610.
9. Father CH, Bevers M (2002) Patchy reaction-diffusion and population abundance: The relative importance of habitat amount and arrangement. American Naturalist 159: 40–56.
Habitat Loss Drives Occurrence Patterns of Canada Lynx

10. Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oko 71: 355–366.

11. Swift TL, Hannan SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biological reviews of the Cambridge Philosophical Society 85: 35–53.

12. Radford JQ, Bennett AF (2004) Thresholds in landscape parameters: occurrence of the white-browed treecreeper Climacteris affinis in Australia. Biological Conservation 117: 373–391.

13. Reuman P, Monkóton M, Nikula A, Hurme E, Nivala V (2004) Assessing landscape thresholds for the Siberian flying squirrel. Ecological Bulletins 51: 277–286.

14. Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation - a review. Conservation Biology 5: 18–32.

15. Swihart RK, Lusk J, Duchamp JE, Rickalla CE, Moore JE (2006) The roles of landscape context, niche breadth, and range boundaries in predicting species responses to habitat alteration. Diversity and Distributions 12: 277–287.

16. Fuller AK, Harrison DJ, Vashon JH (2007) Winter habitat selection by Canada lynx in Maine: prey abundance or accessibility? Journal of Wildlife Management 71: 1980–1986.

17. Murray DL, Boutin S, O’Donoghue M (1994) Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. Canadian Journal of Zoology 72: 1444–1451.

18. Vashon JH, Meehan AL, Jakubas WJ, Organ JF, Vashon AD, et al. (2008) Spatial ecology of a Canada lynx population in northern Maine. Journal of Wildlife Management 72: 1479–1487.

19. Homayack JA, Harrison DJ, Litvaitis JA, William B (2000) Quantifying densities of snowshoe hares in Maine using pellet plots. Journal of Wildlife Management 64: 74–80.

20. Litvaitis JA, Sherburne JA, Bissonette JA (1983) Influence of understory characteristics on snowshoe hare habitat use and density. Journal of Wildlife Management 49: 866–873.

21. Aubry KB, Koehler GM, Squires JR (2000) Ecology of Canada lynx in southern boreal forests. In: Ruggiero LF, Aubry KB, Buskirk SW, Koehler GM, Krebs CJ et al., editors. Ecology and Conservation of Lynx in the United States: University Press of Colorado, Niwot, USA. pp. 373–396.

22. Steury T, Murray DL (2004) Modeling the reintroduction of lynx to the southern portion of its range. Biological Conservation 117: 127–141.

23. Murray DL (2000). A geographic analysis of snowshoe hare population demography. Canadian Journal of Zoology 78: 1207–1217.

24. Poole KG (2003) A review of the Canada lynx, Lynx canadensis, in Canada. Canadian Field Naturalist 117: 360–376.

25. Cheng E, Hodges KE, Melo-Ferreira J, Alves PC, Mills LS (2014) Conservation implications of the evolutionary history and genetic diversity hotspots of the snowshoe hare. Molecular Ecology 23: 2929–2942.

26. Koen EL, Bowman J, Murray DL, Wilson PJ (2014) Climate change reduces genetic diversity of Canada lynx at the trailing range edge. Ecography 37: 754–762.

27. Murray DL, Steury TD, Roth JD (2008) Assessment of Canada lynx research and conservation needs in the southern range: another kick at the cat. Journal of Wildlife Management 72: 1463–1472.

28. Peers MJ, Wielgus M, Thomson DH, Murray DL (2012) Reconsidering the specialist-generalist paradigm in niche breadth dynamics: resource gradient selection by Canada lynx and bobcat. PloS one 7: e134180–e134180.

29. Peers MJ (2001) Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. Biological Conservation 100: 125–136.

30. Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16: 480–492.

31. Peers MJ, Thornton DH, Murray DL (2012) Reconsidering the specialist-generalist paradigm in niche breadth dynamics: resource gradient selection by Canada lynx and bobcat. PloS one 7: e134180–e134180.

32. Peers MJ, Wielgus M, Thomson DH, Murray DL (2014) Prey switching as a means of enhancing persistence in predators at the trailing southern edge. Global Change Biology 20: 1126–1133.

33. OMRN (2011) Annual Report on Forest Management 2009/10: 106–106 p.

34. Cleverger AP, Wierczochowski J, Chruszcz B, Gumon K (2002) Identifying wildlife habitat linkages and planning mitigation passages. Conservation Biology 16: 303–314.

35. LaRue MA, Nielsen CK (2008) Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. Ecological Modelling 212: 372–381.

36. Mogat G, Slough B (2003) Habitat preference of Canada lynx through a cycle in snowshoe hare abundance. Canadian Journal of Zoology 81: 1736–1745.

37. Hoving CL, Harrison DJ, Krohn WB, Joseph RA, O’Brien M (2005) Broad-scale predictors of Canada lynx occurrence in eastern North America. Journal of Wildlife Management 69: 739–751.

38. Bayne EM, Boutin S, Moss KA (2008) Ecological factors influencing the spatial pattern of Canada lynx relative to its southern range edge in Alberta, Canada. Canadian Journal of Zoology 86: 1189–1197.

39. Burdett CL, Moen RA, Nemaj GM, Mech LD (2007) Defining space use and movements of Canada lynx with Global Positioning System telemetry. Journal of Mammalogy 88: 457–467.

40. Holloway GL, Nayler BJ, Watt WR (2004) Habitat relationships of wildlife in Ontario. Revised habitat suitability models for the Great Lakes-St. Lawrence and Boreal East forests. 110p–110p p.

41. Maxie AJ, Hussey KF, Low SJ, Middel KR, Pond BA, et al. (2010) A comparison of forest resource inventory, provincial land cover maps and field surveys for wildlife habitat analysis in the Great Lakes – St. Lawrence forest. The Forestry Chronicle 86: 77–86.

42. Bonn A, Schroder B (2001) Habitat models and their transfer for single and multi species groups: a case study of carahids in an alluvial forest. Ecography 24: 483–496.

43. Tischendorf L, Fahrig L (2000). On the usage and measurement of landscape connectivity. Oko 90: 7–19.

44. Grevez EH, Greco SE (2007) How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. Landscape Ecology 22: 1131–1142.

45. Mowat G, Poole KG, O’Donoghue M (2000) Ecology of lynx in northern Canada and Alaska. In: Ruggiero LF, Aubry KB, Buskirk SW, Koehler GM, Krebs CJ et al., editors. University Press of Colorado, Niwot, USA. pp. 265–306.

46. Walpole AA, Bowman J, Murray DL, Wilson PJ (2012) Functional connectivity of lynx at their southern range periphery in Ontario. Canadian Landscape Ecology 27: 761–773.

47. Jaeger JG (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landscape Ecology 15: 115–130.

48. Grevez E, Thorne J, Berry A, Jaeger J (2008) Integration of landscape fragmentation analysis into regional planning: A statewide multi-scale case study from California, USA. Landscape and Urban Planning 86: 205–218.

49. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: Springer, New York, USA.

50. Lewis CW, Hodges KE, Koehler GM, Mills LS (2011) Influence of stand and landscape features on snowshoe hare abundance in fragmented forests. Journal of Mammalogy 92: 561–567.

51. Wursing AJ, Steury TD, Murray DL (2002) A demographic analysis of a southern snowshoe hare population in a fragmented habitat: evaluating the refugium model. Canadian Journal of Zoology 80: 169–177.

52. Roth JD, Marshall JD, Murray DL, Nickerson DM, Steury TD (2007) Geographical gradients in diet affect population dynamics of Canada lynx. Ecology 88: 2736–2743.

53. Barnagaud JY, Devictor V, Jiguet F, Archam F (2011) When species become generalists: on-going large-scale changes in bird habitat specialization. Global Ecology and Biogeography 20: 630–640.

54. Allard-Duchene A, Pothier D, Dupuch A, Fortin D (2014) Temporal changes in the landscape context, niche breadth, and range boundaries in predicting species responses to habitat alteration. Diversity and Distributions 12: 277–287.

55. Crooks KR, Burdett CL, Theobald DM, Boitani L (2011) Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philosophical Transactions of the Royal Society B:Biological Sciences 366: 2642–2651.