Southern range dynamics of Canada lynx over seven decades

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Abstract

The range of the Canada lynx (*Lynx canadensis*) has contracted substantially from its historical range prior to the 19th century. Using harvest records, we found that the southern range of the lynx in Ontario in the late 1940s collapsed and then in a short period of time increased to its largest extent in the mid-1960s where the lynx range spread south of the boreal forest for a decade. After this expansion the southern range contracted northwards beginning in the 1970s. Most recently, there has been a slight expansion between 2010-2017. We have attributed these dynamics on the southern range periphery to the fluctuation of the boreal lynx population in the core of the species' range. In addition, connectivity to boreal lynx populations and snow depth seemed to condition whether the lynx expanded into an area. However, we did not find any evidence that would suggest that these changes were due to anthropogenic disturbances or competition. The boreal lynx population does not reach numbers as it once did, consequently we likely will not see large expansions of the southern lynx range as in the mid-1960s. Our results suggest that southern lynx range in Ontario have been driven by the magnitude of the boreal lynx population cycle, connectivity to the boreal forest and snow conditions. Therefore, it is quite unlikely that southern lynx population in the Great Lakes will ever recover, since the warming climate and forestry practices are causing a northward contraction of the boreal forest and likely with it the core lynx populations.

Introduction

Over the past century the range of many species has changed, often attributed to climate change and land cover modification (Thomas 2010, Laliberte and Ripple 2004, Walther *et al* 2002). A species can respond to environmental changes by exploiting resources at the extremities of its niche breadth (Sexton *et al.* 2017), by phenotypic plasticity (Valladares *et al.* 2014, Nicotra *et al.* 2010), or by adaptation (Williams *et al.* 2008). However, the rate at which current conditions are changing might make adaptation impossible for many species because the process of natural selection is too slow (Davis and Shaw 2001). Consequently, species will have to track their bioclimatic niche (Visser 2008) the ability to do so will be an essential characteristic influencing future biodiversity (Bell and Gonzalez 2011, Schloss *et al.* 2012, Travis *et al.* 2013).

Terrestrial species that have ranges near the poles will be limited in their ability to track climate because they are limited by the availability of space to move to higher latitudes (Kerr and Packer 1998). Therefore, many unique cold adapted species will eventually perish unless they somehow adapt to much warmer conditions and to new biotic interactions. Understanding how and why the warmer range edge of cold adapted species has been changing would help us in making better informed conservation decisions, since anthropogenic change is not slowing down.

The Canada lynx (*Lynx canadensis*) is an iconic carnivore that largely resides in the boreal forest of North America and its northern range has some expansion potential into northern taiga landscapes but is generally bounded by tundra and the Arctic Ocean (Poole 2003). The lynx is a habitat specialist because it

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almost exclusively preys on snowshoe hares in the boreal forest (O'Donoghue *et al.* 1998). Consequently, its population dynamics are highly coupled to the 8-11 year population cycle of the snowshoe hare, mirroring it with a 1-2 year delay (Poole 2003). Since presettlement times the Canada lynx range has contracted by 40% (Laliberte and Ripple 2004). However, most of this range reduction took place prior to the 20th century and was attributed to unregulated harvest and habitat loss due to land clearing during European colonization (de Vos 1952, de Vos 1964, Hoving *et al.* 2003, McKelvey 2000, Poole 2003).

Canada lynx are predominantly found in areas where snowshoe hare density is above 0.5 per hectare (Zahratka and Shenk 2008, Hodges *et al.* 2009, Berg *et al.* 2012, Ivan *et al.* 2014). In the southern periphery of the lynx range, hare population densities have declined compared to historic levels (Aubry *et al.* 2000, Hodges 2000, Murray 2000) and this most likely accounts for the contraction of the lynx from its historic range (Poole 2003). Following years with high peak hare abundance, Canada lynx appear to migrate from range core to range periphery as a result of density dependent dispersal (McKelvey et al. 2000). Such dispersal pulses might lead to higher occupancy of the southern range periphery (McKelvey et al 2000, Murray *et al.* 2008). Consequently, lower peaks in hare abundance might decrease the likelihood of dispersal of lynx into the southern periphery (Poole 2003). Southern dispersal might also be limited in some locations by connectivity with the range core (Ruggiero *et al.* 2000, Buskirk 2000, Walpole *et al.* 2012).

The warming climate might indirectly impact the lynx through its main food source the snowshoe hare. The timing between molt and season change for the snowshoe hare is important in decreasing predation rates (Zimova *et al.* 2016). A changing snow regime could increase snowshoe hare predation rates by increasing the rate of mismatch between snowshoe hare molt and season change. Increased predation rates might also reduce the amplitude of the hare cycle (Krebs 2010).

Climate change will also open formerly inhospitable habitat to new species in the lynx range. Bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) have smaller feet than Canada lynx, consequently they cannot support as much weight as lynx in deep snow without sinking (Parker *et al.* 1984). This might be one factor that has hindered the bobcat from invading Canada lynx territory in the past (Marston 1942, McCord 1974, Murray *et al.* 2008, Parker *et al.* 1984). However, since the climate is warming, and snow depths across the southern periphery of the lynx range are shallower, southern competitors might be less hindered by snow, increasing their competitive potential (Buskirk *et al.* 2000, Ruediger *et al.* 2000, Scully *et al.* 2018). In fact, Parker *et al.* (1984) found that after several years of low snow the bobcat invaded the lowlands of Cape Breton while the Canada lynx left the area. Marrotte *et al.* (2020a) found that deep winter snow in the Great Lakes region limited bobcat expansion northward, suggesting that greater expansion will result from additional climate warming.

The lynx once occurred in 24 of the United States (McKelvey 2000), but currently only occurs in 7 (US Fish and Wildlife Service 2017). As a result, the lynx is designated as 'threatened' in the contiguous United States (US Fish and Wildlife Service 2000). Despite the range contraction, its protection status is being debated and it might be removed from the list of endangered species in the United States. In Canada, the lynx occupies 95% of its historic range (Poole 2003). However, it is designated as provincially endangered in Nova Scotia (Parker 2001), and New Brunswick (New Brunswick Endangered Species Regulation 2013) and was extirpated from Prince Edward Island (Poole 2003). Further analysis has demonstrated that the range of lynx in British Columbia has been stable since the 1930s (Gooliaff and Hodges 2018). In contrast, the lynx range in Ontario appears to have contracted northwards by 175 km from 1972 to 2010 (Koen *et al.* 2014).

We estimated the past extent of the Canada lynx southern range in Ontario, Canada using harvest records and then determined whether the spatial-temporal patterns could be attributed to snowshoe hare and boreal lynx population dynamics, connectivity, climate, land use and competition. We predicted that years with low Canada lynx abundance in the boreal forest were associated with a reduction in the extent of the southern lynx range. We also predicted that areas with high human disturbance, shallow snow, presence of competitors, and with low connectivity to boreal lynx populations were less likely to be part of the southern range.

Material and Methods

Study Area

We defined the southern periphery of the lynx range as the southern margin of the boreal forest to areas south of the boreal forest where lynx occurred at least once between 1948-2017 in Ontario, Canada (Figure 1). To first identify the boreal forest, we used the spatial layer supplied by Natural Resources Canada that were derived from maps from the early 1970s to the late 2000s (Brandt 2009). We then defined our study area as the region where lynx have occurred south of the boreal forest and an additional band of southern boreal forest that extended 1 sampling unit (defined below) or 65 km north of the southern boundary of the boreal forest to account for uncertainty in both the boreal limit and the uncertainty in our harvest records. There were 3 distinct southern range zones in Ontario. The west and central zones are separated by Lake Superior and are also within 100 km of the boreal forest, whereas the east zone is further away. We used these zones to illustrate regional trends in range change, since these zones had different spatial and temporal patterns.

The southern lynx range periphery was predominantly found in the Great Lakes-St Lawrence Forest, which is a transition zone between the boreal and deciduous forest (Boucher *et al.* 2009). The Great Lakes-St Lawrence forest is dominated by white pine (*Pinus strobus*), red pine (*Pinus resinosa*), hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*) (Rowe 1972).

Harvest records

Long term spatial data on terrestrial species are quite rare. Fortunately, wildlife agencies track furbearer harvest each year. Such records contain important information that can be used to monitor and study the change in range, spatial distribution, and population dynamics of several species that are harvested for their fur (Hayne 1949, Viljugrein *et al.* 2001).

Ecologists have used fur harvest data to address fundamental questions in ecology (Krebs *et al.* 1995, Keith 1963, Bulmer 1974, Elton and Nicholson 1942). There are, however, some issues with using fur returns. Trapping effort should be accounted for (DeVink *et al.* 2011, Dorendorf *et al.* 2016) and generally the location of capture is only available at a coarse geographic level.

The Ontario Ministry of Natural Resources and Forestry has been compiling furbearer trapping records since the beginning of the 20th century (Figure 2). A registered trapline system in Ontario began in the late 1940s, and therefore, spatially referenced annual harvest records are available beginning in 1947. Trapping of furbearers in Ontario takes place within a township or on a trapline. Traplines are designated as areas on public land where trappers are licensed to harvest furbearers. Hereinafter we refer to townships and traplines as trapping units. We georeferenced these records using the appropriate trapping unit map for each harvest record.

Spatial and temporal coverage

Boundaries of trapping units changed occasionally due to regulation changes. Therefore, we divided the southern Canada lynx range into 370 equal area hexagons or sampling units of 2,731 km^2. The area of these hexagons was based on the largest trapping unit found in the southern range between 1947 and 2017. We assigned each trapping unit to the hexagon that its centroid fell into. All the information in each trapping record was then aggregated to the sampling unit for each year. Of the 370 sampling units only 146 contained southern boreal trapping units. There were years where records were completely missing for all sampling units (1969, 1970, 1975, 1986, 1989 and 1991), years where many records were missing (1947, 1972 and 1992) and other years where certain sampling units had the occasional missing record. Consequently, temporal coverage of sampling units varied from 65 years to only 4 years for the 71-year period between 1947-2017.

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Due to the variability of spatial and temporal coverage, we restricted our analysis to sampling units that had good temporal coverage. We first restricted our analysis between 1948 and 2017, because the trapline system was not completed yet in 1947 and therefore had limited spatial coverage. We further restricted our analysis to sampling units that had at least one lynx that was harvested from 1948 to 2017. Next, we omitted sampling units that had > 5 years of consecutive missing data or at most 10 years of missing records. This left us with 82 of the previous 146 sampling units. Finally, we removed sampling units that contained on average less than 1000 km^2 of trapping unit surface area between 1948-2017. These sampling units were all found either near the periphery of large water bodies, near political boundaries or near an area that had trapping restrictions (Provincial Parks or crown game preserves). This left us with a final sample size of 65 sampling units.

Estimating the spatial and temporal range

We used the R package 'mgcv' to fit Hierarchical Generalized Additive Models to estimate the probability of harvesting a Canada lynx within sampling units across space and time (Woods 2011). We first built several models that combined our effort predictors. We used thin plate smoothers for each predictor, since we expected a non-linear relationship. We also compared two different spatial-temporal tensor product smoothers (Augustin *et al.* 2013, Wood *et al.* 2013, Eickenscheidt *et al.* 2018, Zhou *et al.* 2019). In each spatial temporal structure, we modelled the yearly temporal variability with a cubic regression smoother. The spatial structure was modelled with a spatial discrete process using a Markov Random Field (MRF) or a thin plate (TP) smoother on the spatial coordinates.

We used Relative Maximum Likelihood to fit our models. We set the number of knots 'k' to 5 for each effort predictor, to 65 for all spatial smoothers and to 40 for the year smoother. We set the spatial and temporal knots to high values based on our highest computational capabilities. However, the 'gam' function in the mgcv package will fit models using penalised likelihood to estimate parameters for each basis function, therefore increasing the number of knots simply makes computation longer and does not overfit the model. Some basis functions may be penalised to the point where their estimates are zero in the final model fit (Petersen *et al.* 2019).

We then estimated the range of the Canada lynx across space and time by predicting the probability of trapping a lynx with an average value of effort. We identified the areas that had at least a 50% chance of harvesting a Canada lynx for each year between 1948 and 2017.

Trapping effort covariates

We investigated 3 types of effort measures: trapping area or frequency, harvest, and market-based measures. Our trapping area or frequency-based measures were the total number of trapping units and the area covered by trapping units within each sampling unit each year. Our first harvest-based effort measure was the total number furbearers harvested. We also thought that the density of American marten *(Martes americana*) harvested on a trapline would be a good measure of trapping effort, since martens are sympatric with lynx, the fur is valuable, and might index trapper effort (Webb *et al.* 2008). The price of lynx fur is also an important factor that can govern harvest patterns of lynx (DeVink *et al.* 2011, Dorendorf *et al.* 2016). Our market-based measure was the average lynx pelt price from the previous year.

For all animal-based measures of effort we investigated the log of the absolute number, density, and the average number of animals across trapping units, since the number of animals trapped varied exponentially between trapping units. In total we had 9 effort predictors, but we did not investigate models that combined total furbearer harvest and American marten harvest, since these measures were not independent. We also only investigated models that included the total number of trapping units, the area occupied by those trapping units, and the average pelt price. Consequently, we compared 6 different effort models to find the best model that would likely account for effort bias in harvesting a lynx.

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We calculated the yearly average price of lynx pelts that originated from Ontario using the fur-return summaries from a variety of sources. We gathered summaries collected by Statistics Canada (http://www5.statcan.gc.ca; CANSIM Table 003-0013). The time series ranged from 1970 to 2011, but most of the data from 2010 to 2017 were missing. Therefore, we used summaries provided by the Fur Institute of Canada for 2010-2017 (www.fur.ca). We then added data from the earlier period 1948 to 1970 provided by Novak (1987a and 1987b).

We then corrected for inflation using the Consumer Price Index (CPI) for the province of Ontario also available on the Statistics Canada website (statcan.gc.ca; CANSIM Table 326-0021). For each year we multiplied the average pelt price by the 2019 CPI and divided these values by the CPI of their appropriate year. This adjusted the average pelt prices to 2019 Canadian Dollars. In our analysis we used the adjusted average pelt price of the previous year for the current year of observation. The assumption is that trappers observed a high pelt price and are more likely to harvest a lynx in the following year.

Testing hypotheses of range change

We were interested in understanding how the area of the southern range fluctuated over space and time in accordance with different hypotheses. To simplify our analyses, we broke up our subsequent analyses into both spatial and temporal tests.

To test spatial hypotheses, we summed the number of times each sampling unit was part of the lynx range between 1948-2017. We then compared these values to each spatial predictor while we controlled for the influence of all other predictors with a partial Spearman rank correlation. We used a nonparametric correlation coefficient, because the response variable and all the covariates were not normally distributed. To test our temporal hypotheses, we calculated the area occupied by the southern lynx range each year and compared each temporal predictor to this time series. We investigated temporal lags of up to 2 years. Temporal stationarity is an important assumption for the association metric to be valid, therefore we calculated the between year differences for all time series (Priestley 1988). We then estimated associations with a Pearson correlation coefficient. We resampled without replacement our observations 9999 times to calculate p-values. We then adjusted our p-values to account for multiple tests using a Bonferroni correction.

Spatial and temporal predictors

We calculated the distance to boreal forest by summing the straight-line distance between the edge of each sampling unit and the closest boreal forest. For human disturbance we used the major roads in the Ontario Road Network layer as a proxy variable (LIO; geohub.lio.gov.on.ca). For each sampling unit we calculated the distance to the nearest road in kilometres.

We estimated a hare time series by gathering hare abundance data from the Ontario Ministry of Natural Resources and Forestry (OMNRF Unpublished). Monitoring of hare populations is undertaken in the fall (October) through an array of pellet count plots in several locations across the province (e.g., Bendell and Young 1995). The longest running snowshoe hare population monitoring (since 1986) is in Gogama, Ontario (Figure 1). These data originated from many plots that we aggregated to a single measure that indicates the average number of hare pellets. The number of pellets should indicate the density of hare found in nearby boreal forest (Krebs et al. 2001).

We built the boreal forest lynx population time series by gathering all trapping records located in the boreal forest and summed these by year. We wanted our boreal lynx population index to be independent from our response data, therefore we removed all records used to estimate the lynx range that were outside of the boreal forest (i.e. , all records within our hexagonal study areas). We also ln-transformed these boreal lynx harvest values to correct for harvest bias (Royama 2012).

We built a snow map and time series from weekly measurements gathered from the Snow Network for Ontario Wildlife (wildliferesearch.ca/snow; Warren et al. 1998). For each year, we calculated the SDI (Snow

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Depth Index), which is the sum of all weekly measurements collected at a station over the winter months. We interpolated the data across our study area using ordinary kriging using the 'automap' package in R (Hiemstra and Hiemstra 2013). We then calculated the average SDI for each sampling unit for our spatial map and we calculated the average annual SDI for each year between 1952 and 2017. We removed stations that had less than 16 measurements during the year. This is equivalent to 4 months of winter and captured some early spring and late fall snow events.

We built maps of the occurrence of competitors and their associated time series by counting the number of times each species (bobcat and coyote) was present in the harvest records in each sampling unit over time and space. For our spatial map we summed the number of years that a competitor was found in each sampling unit. For our time series we summed the number of sampling units that each species was present in during each year.

We performed all our spatial processing and modelling in R version 5.5.1 (R Core Team 2014). All spatial layers were projected to MNRF Lambert conformal conic (EPSG:3161).

Results

The model that could best account for the effort of harvesting a Canada lynx and the spatial temporal process in the southern periphery of Ontario, Canada included the log transformed total number of furbearers harvested and a thin plate smoother on the spatial coordinates (Table S1). This model was 20.914 AIC units lower than all other models and its AIC_w was 1.000. The spatiotemporal effort model had an adjusted R^2 of 0.586 and a deviance explained of 54.1%. Other than the total number of furbearers harvested, the 3 other effort related predictors followed linear relationships (Figure S1). The additive effect of the number of trapping units, the total area, and the average price were not as important than the total number of animals harvested. The probability of harvesting a lynx decreased with the total area harvested while the 3 other predictors had a positive relationship. Also, the influence of lynx pelt price was weak compared to the other predictors.

The probability of harvesting a Canada lynx south of the boreal forest across Ontario changed through time (Figure 3). During the late 1940s and the early 1950s, the likelihood of harvesting a lynx was at its lowest. However, in the mid-1960s the odds peaked across the southern range and even trapping units found in the east had a high probability. After this peak lynx period, it then became unlikely to harvest a lynx in the east and this pattern continued to 2017. The odds of harvesting a lynx peaked in both the west and central zones in the early 1960s and again in the mid-1970s, then declined until the 2000s and increasing slowly until 2017 to an overall probability of harvest higher than in previous years.

To get a better idea of the range dynamics, we calculated the occupied area of the southern range of each zone for each year (Figure 4). In 1950 the total extent of the southern lynx range was at its lowest and occupied a total are of 19,118.2 km^2. The extent of the range peaked between 1963-1964 and occupied a maximum area of 147,483.5 km^2. This was an area 7.7x larger than during the crash in the late 1940s. From 1970 onwards, the southern range varied much less in size compared to previous years. It declined between 1970 and the late 1980s, but gradually increased until 2017 to a size comparable to the early 1970s. There were also a few notable decreases in range in the periods 1965-1972, 1983-1992 and 1995-2002.

In general, all 3 zones (west, central, and, east) followed similar patterns. However, from 1957 to 1964 the east zone increased from 5,462.4 to 30,042.9 km^2, which was a 6-fold increase and occupied most of the Lanark and Renfrew County just east of Ottawa (Figure 3). This increase was not as dramatic in the west and central zones, where there was only a 1.5- and 1.3-fold increase. Although, these two northernmost ranges were already closer to their maximum extent of 65,548.2 and 54,623.5 km^2, consequently they could not have increased as intensely during this period. A smaller range contraction in this same Lanark and Renfrew County area also occurred in 1971 to 1973.

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From the late 1950s to 2017, the west and central zones varied by 24,580.6 [40,967.6-65,548.2] and 16,387.0 km^2[38,236.5-54,623.5]. The west zone reached its maximum area more recently in 2013 and 2017, whereas the central zone reached its maximum area multiple time in the periods 1960-1967 and 1970-1976. The east zone varied quite differently. It increased dramatically twice in the period 1959-1973 and never reached these levels again. After this point the range varied between 0 and 8,193.5 km^2.

We calculated the number of years each sampling unit was within the lynx southern range. Sampling units in the south were less frequently part of the Canada lynx range (Figure S2). In the east zone, sampling units were only part of the range on average 8.7 years over the 70-year time period. In contrast, the west and central zones were part of the range 48.2 and 58.1 years, respectively.

We predicted that undisturbed areas with deep snow, an absence of competitors, and close proximity to the boreal forest were more likely to be part of the southern range. We found that 2 of 5 of these relationships met our initial expectations (Table 1). Sampling units that were more frequently found within the Canada lynx range were closer to the boreal forest and had deeper average annual snow. We also predicted that years with large numbers of hare and lynx in the boreal forest, low number of competitors, and deep snow increased the extent of the southern Canada lynx range. We found that only 1 relationship met our initial expectations (Table 1); when the number of Canada lynx in the boreal forest increased, the area of southern range increased the following year.

Discussion

We predicted that years with low Canada lynx abundance in the boreal forest were associated with a reduction in the extent of the southern lynx range. We found support for this idea, as it appeared that the southern range dynamics were mostly driven by boreal lynx population dynamics. The probability of harvesting a lynx at the southern periphery was predicted by lynx harvest the year earlier in the core boreal range. We also predicted that areas with high human disturbance, shallow snow, presence of competitors, and with low connectivity to boreal lynx populations were less likely to be occupied as part of the southern range. However, we found that the anthropogenic effect of roads and competition from bobcats and coyotes did not seem to have influenced the southern range of the Canada lynx in Ontario. We did find that areas that had deep winter snow were often found within the southern lynx range. However, this relationship did not vary temporally with the area of the southern lynx range (Table 1). We used this snow depth predictor as an index of climate change, since we thought that the highest impact of climate warming on lynx would be related to the timing of molt of its main prey the snowshoe hare. We also thought that competition would arise in areas with less snow over time and would become more hospitable to coyote and bobcat. However, we found that the average annual snow depth was not driving the temporal dynamics of the lynx southern range in Ontario but is a habitat condition that determines whether lynx will expand into an area.

There was a weak signal for the temporal dynamics of the coyote, but we did not have enough power to detect a significant relationship given number of tests we performed (Table 1). It is quite reasonable to think that the coyote is a competitor because they are generally found across the southern range apart from a few areas within the boreal forest in Ontario (Figure S3). Bobcat on the other hand, occupied a very small area and generally occurred in the southeastern corner of the west and northeast zones (Figure S4). This spatial relationship itself indicates that the bobcat is not responsible for the range contraction in the southeastern zone, since it is rarely found there. Recent finer scale studies suggested segregation between lynx and bobcat (Marrotte et al. 2020b, Morin *et al.* 2020).

We observed that the southern range of the lynx has recovered from a dramatic decline in the late 1940s (Figure 4). It has never returned however, to the short-lived maxima we observed during the 1960s. More recently, in the period 2012-2017, the range has reached its maximum extent in the west and central zones. After the mid-1980s, the southern range varied less and from 2010 to 2017, seemed to be increasing. Consequently, we did not find the substantial range loss in more recent times that has been observed in parts

of the contiguous United States (Ruediger *et al.* 2000), and as in a previous analysis in Ontario (Koen *et al.* 2014). The stable and somewhat increasing range in Ontario is not unique across the lynx range, since lynx are increasing in numbers in Maine, USA (Simons-Legaard *et al.* 2016) and the lynx range in British Columbia has been stable since 1935 (Gooliaff and Hodges 2018). It is important to remember however, that the Canada lynx range across all of North America has contracted substantially from its presettlement extent (Laliberte and Ripple 2004).

The extensive contraction in the early part of the time series may have extended from 1938 to 1951 (Figure 2). In fact, de Vos and Matel (1952) noted that lynx occurrences were rare at this time and the range was also gradually shrinking. They attributed this decline to ecological changes and overharvesting. The decline prompted the closing of lynx trapping during 1951-1952 season and a quota system for lynx was established and trapping was reopened the next year (de Vos and Matel 1952). At the same time, in all of Canada, harvest dropped from 33,054 pelts in 1925 to only 3,734 lynx pelts in 1949 (de Vos and Matel 1952). Lynx fur returns for each jurisdiction in Canada were an order of magnitude lower during the population crash. In approximately the same period, lynx occurrences and harvest in Wisconsin, Minnesota and Michigan also dropped (McKelvey 2000).

Immediately after this large continental wide population crash and subsequent range contraction, the southern range in Ontario expanded almost 8-fold (Figure 4). The ranged peaked in 1963-1964 and lynx were being harvested more than 100 km south of the boreal forest in southern Ontario for almost 10 years (Figure 3). At the same time there was an increase in fur returns and occurrences of lynx in the Great Lakes states immediately south (McKelvey 2000). Similar range expansion and population increase were also present in Alberta, British Columbia, Saskatchewan, Manitoba and Quebec during this period (Todd 1985, McKelvey 2000).

These earlier large fluctuations of the southern lynx range in Ontario and harvest in the Great Lakes states were likely driven by immigration of lynx from the boreal forest (McKelvey 2000, Steury and Murray 2004, Murray *et al.* 2008). We do see this pattern in our analysis; the southern lynx range changes with the population dynamics of the boreal lynx and this influence decays away from the boreal forest (Table 1). Density dependent dispersal from the boreal forest likely drives the southern lynx range in the northern Great Lakes region. Consequently, southern populations appear to be maintained by emigration from sources in the range core (Steury and Murray 2004, Murray *et al.* 2008). During peak years, individuals venture south and colonize marginal habitat outside of the boreal forest in Ontario and eventually reach the northern Great Lakes states (Mech 1973, Mech 1980). In more recent times in Ontario, the boreal lynx cycle did not reach extremes as it once did (Figure S5), therefore lynx populations south were no longer being rescued.

There was a period of slow range contraction from 1970 to the late 1990s, where lynx appeared and quickly disappeared from their southern Ontario range. This period is not unique to Ontario, most jurisdictions followed the same pattern (McKelvey 2000). In an earlier study, Koen*et al.* (2014) noted that the largest range loss happened in this period, but we did not see a continuous decline after 1991 as they did. In fact, the range expanded, and the west and northeast zones were at their largest possible extent and occupied a combined area that was previously unforeseen (Figure 4). Our results probably differ because we were able to assess a longer time series (1972-2010 vs. 1948-2017) and we examined a much larger area.

Conclusion

The southern range in Ontario is strongly driven by the boreal lynx population dynamics and this may mean that migration of lynx south of the Canada-USA border will become increasingly infrequent, since lynx in the boreal forest of Ontario have not recently reached the high numbers they once did. This is even more true given how average annual snow decreases southward across the border. Canada lynx in the northern US Great Lakes states are likely to require populations that are locally sustained, rather than maintained through a rescue effect, as we anticipate that sufficient southward migration will continue to be rare in the

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future due to reduced amplitude of lynx fluctuations and changing environmental conditions.

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Tables

Table 1. Spatial and temporal relationships. Values in bold face are significant. Two-tailed p-values were calculated from 9999 permutations. Spatial relationships are partial correlations. Temporal p-values were adjusted with a Bonferroni correction. We only reported the lags that had the absolute highest coefficient. However, all other lags had an adjusted p-value > 0.05. All partial correlation coefficients are Spearman's rank correlation coefficient and temporal correlations are Pearson's correlation coefficients.

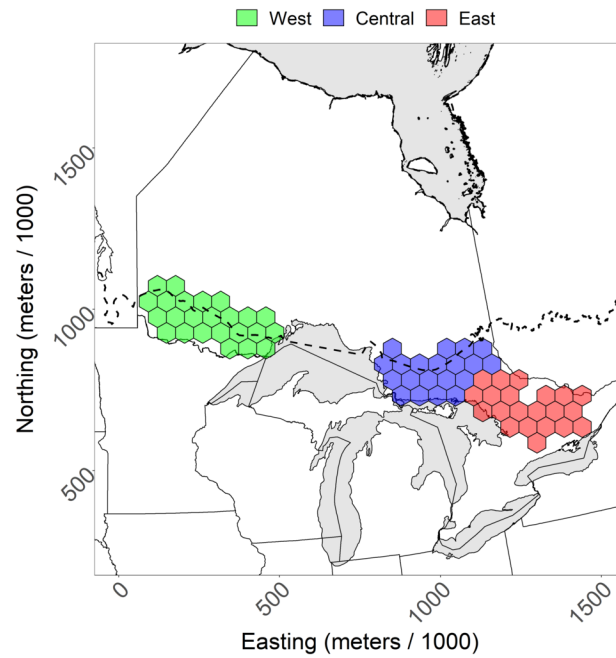| Covariates	Expected relationship	Spatial	Spatial	Temporal	Temporal	Temporal	Tem
		Παρτιαλ ρ	Prob.	ρ	Lag	Prob.	Spa
Distance boreal forest	-	**-0.336**	0.008				
Distance nearest road	+	0.189	0.144				
Average annual SDI	+	**0.454**	0.000	0.129	0	1.000	1952
Bobcat presence	-	0.036	0.783	-0.228	0	1.000	1948
Coyote presence	-	-0.071	0.591	-0.292	0	0.402	1948
Average hare pellets	+			0.337	1	1.000	1986
Boreal lynx harvested	+			**0.504**	1	0.003	1948

Figures

Figure 1. Sampling units in the southern Canada lynx range in Ontario, Canada used to estimate the probability of harvesting a lynx between 1948-2017. The black line is the southern limit of the boreal forest by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).
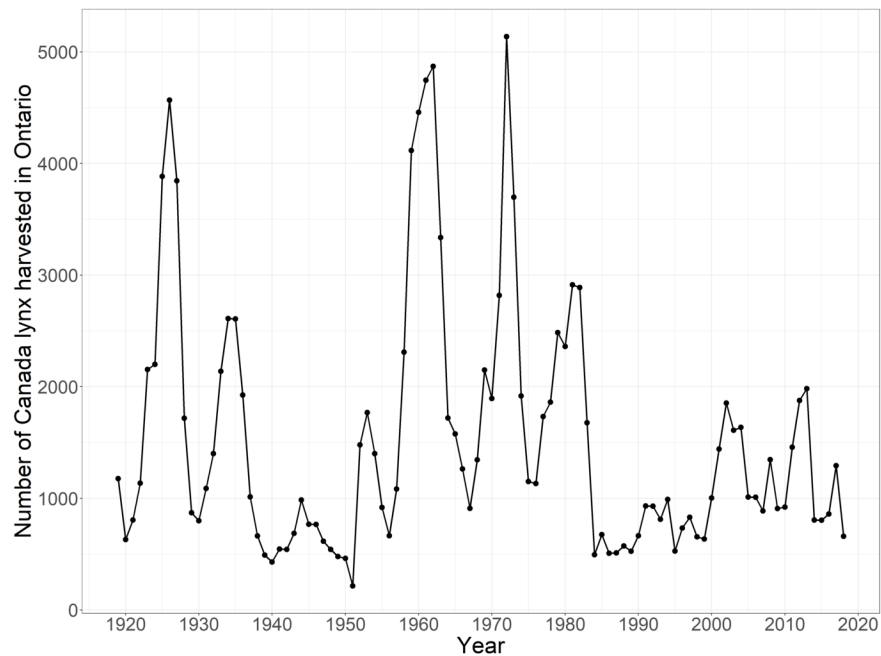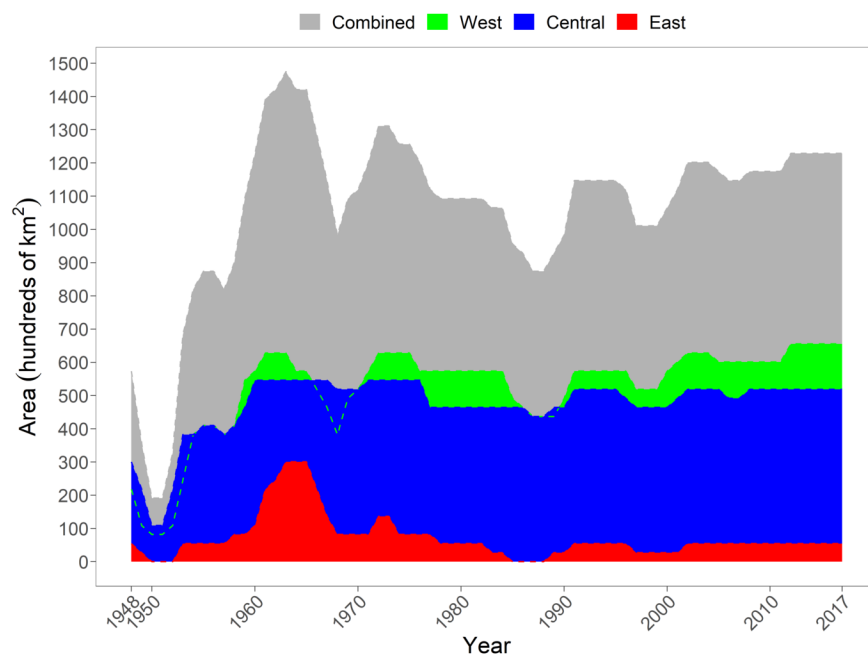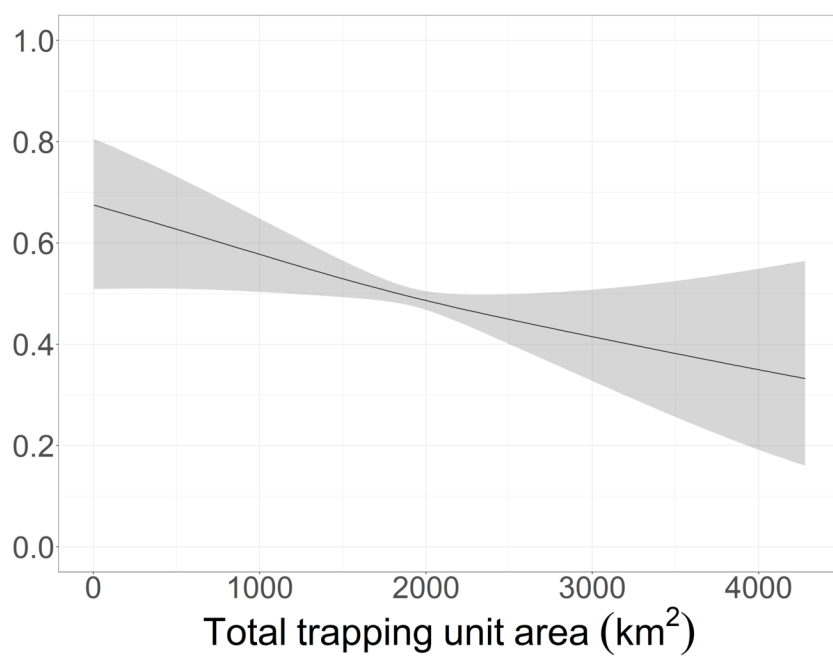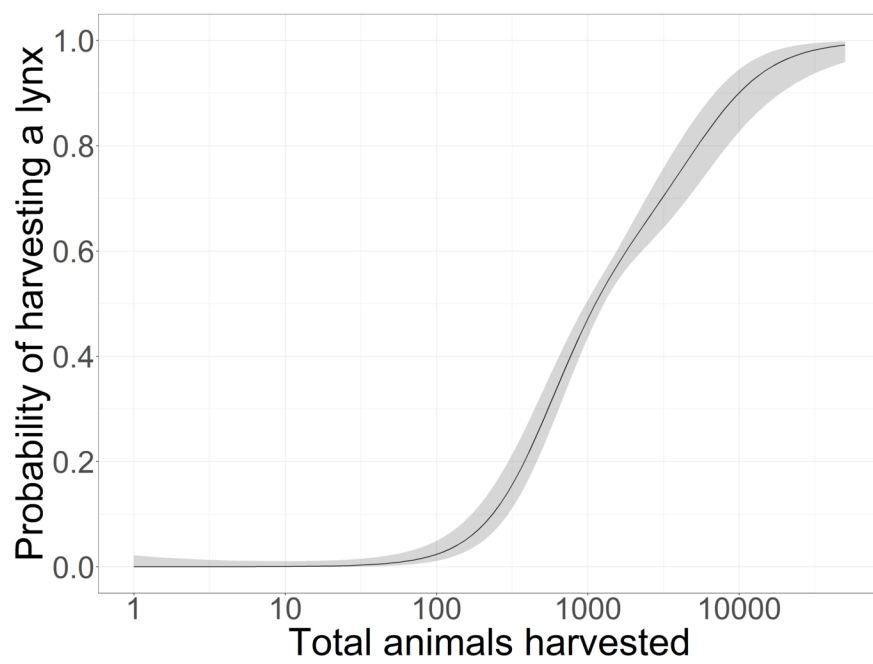
Figure 2. Number of Canada lynx harvested in Ontario, Canada between 1919-2018. Values earlier than 1947 were from Novak (1987a and 1987b). Later values were aggregated from the Ontario fur returns that were used in this study.

Figure 3. Spatial-temporal pattern of the probability of harvesting a Canada lynx from 1948 to 2017 in Ontario, Canada. The black line is the boreal forest southern limit by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).

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Figure 4. Area of the Canada lynx southern range in Ontario, Canada between 1948-2017. The maximum area of the west, northeast and southeast zone was 65,548.2, 54,623.5 and 57,354.7 km^2. The area was calculated by summing the area of the sampling units (hexagons) that had a probability of harvesting a lynx over 0.5.

Supplemental Material

Table S1. Summaries of models used to explain the probability of harvesting a lynx while accounting for harvest effort across sampling units in the southern lynx range between 1948-2017 in Ontario, Canada. Covariates unrelated to animals harvested were also included in each of these models. These were the total number of trapping units, the area occupied by those trapping units and the average pelt price. The spatiotemporal pattern was modelled with a tensor product smoother. We modelled the year of harvest with a cubic regression smoother and the spatial process was modelled with a thin plate smoother on the geographic coordinates or with a Markov random field smoother using the neighborhood structure. Harvest-based effort covariates were ln transformed. MRF is Markov Random Field and TP is Thin Plate smoother.

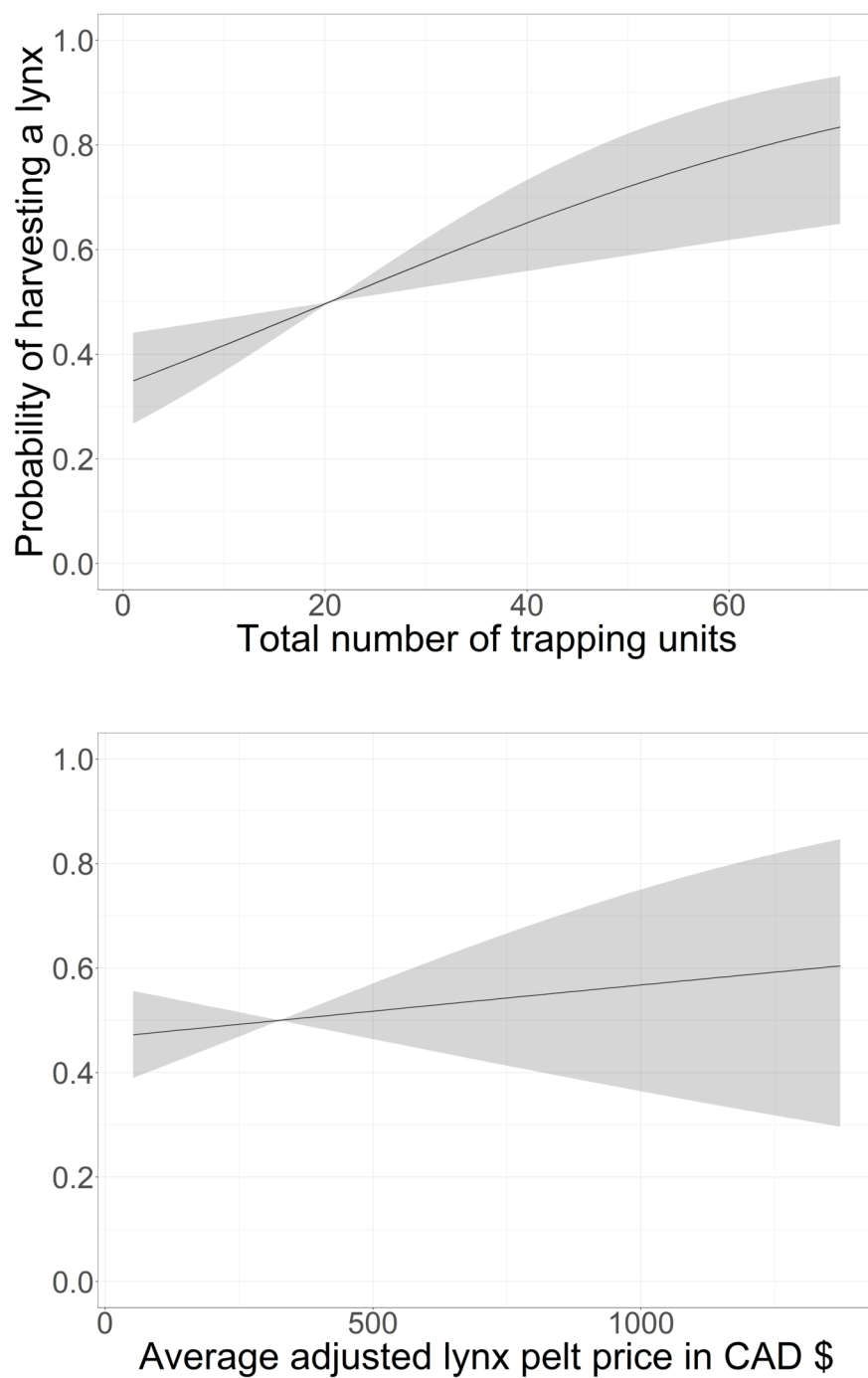| Rank	Harvest-based Covariate*	Spatial Smoother	Relative Maximum Likelihood	Proportion Devianc
1	Total Harvest	TP	1521.568	0.541
2	Average Total Harvest	TP	1533.745	0.538
3	Total harvested Density	TP	1543.371	0.536
4	Marten Harvest Density	TP	1549.976	0.535
5	Marten Harvest	TP	1555.515	0.534
6	Marten Average Harvest	TP	1557.371	0.533
7	Total Harvest	MRF	1611.840	0.583
8	Average Total Harvest	MRF	1618.995	0.584
9	Total harvested Density	MRF	1624.088	0.585
10	Marten Harvest Density	MRF	1616.483	0.582
11	Marten Average Harvest	MRF	1620.269	0.583
12	Marten Harvest	MRF	1620.067	0.582

Figure S1. Effort covariates for predicting the probability of harvesting a Canada lynx between 1948 and 2017 across sampling units south of the boreal forest in Ontario, Canada.
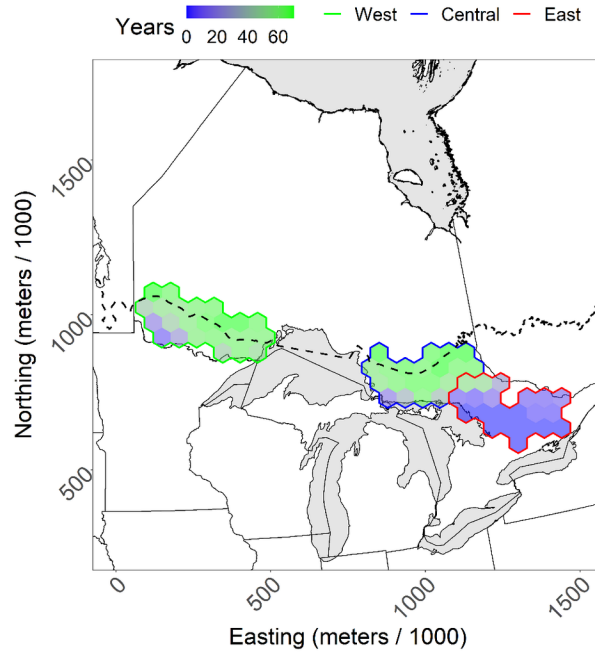
Figure S2. Frequency or number of years that each sampling unit was part of the southern Canada lynx range between 1948-2017 south of the boreal forest in Ontario, Canada. The black line is the boreal forest southern limit by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).
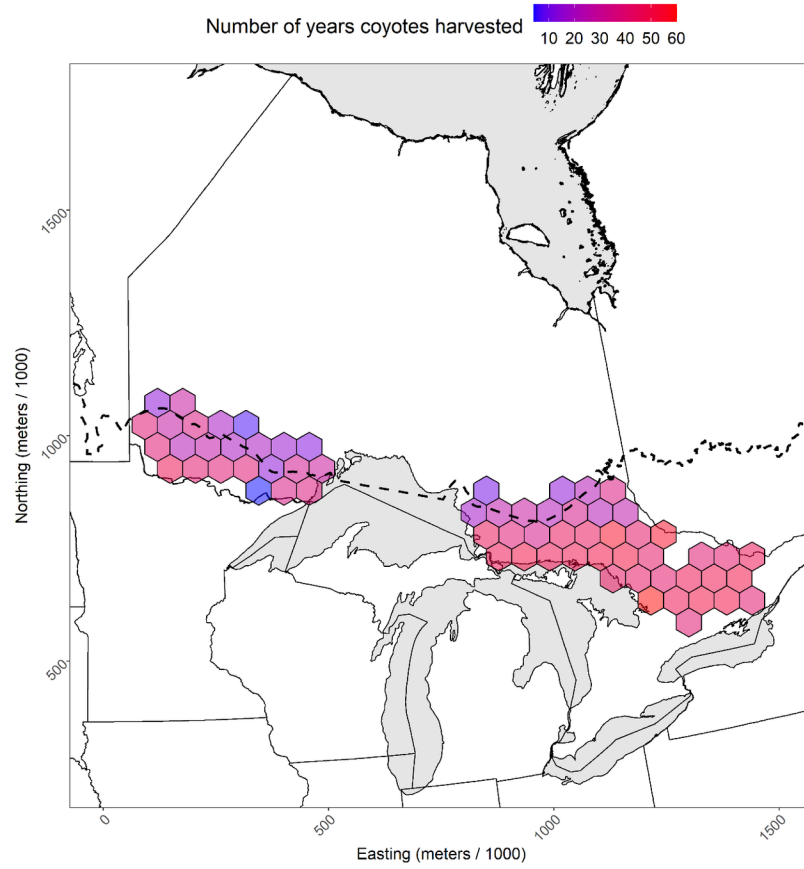
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Figure S3. Number of years that coyotes were harvested within sampling units in the southern range of the Canada lynx in Ontario, Canada between 1948 and 2017. The black line is the boreal forest southern limit by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).
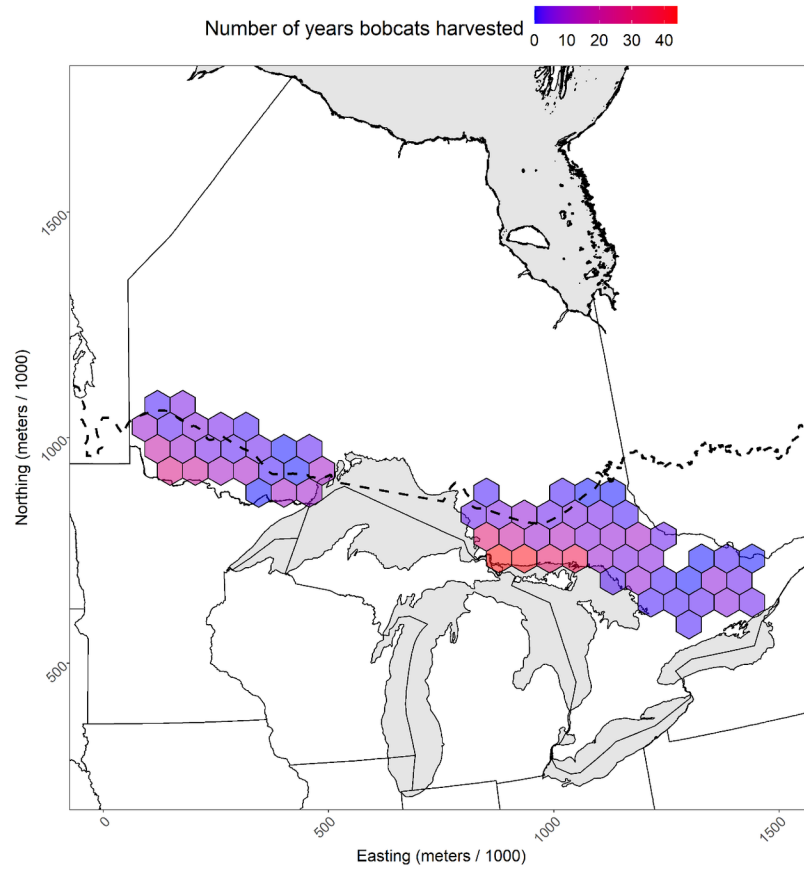
Figure S4. Number of years that bobcats were harvested within sampling units in the southern range of the Canada lynx in Ontario, Canada between 1948 and 2017. The black line is the boreal forest southern limit by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).
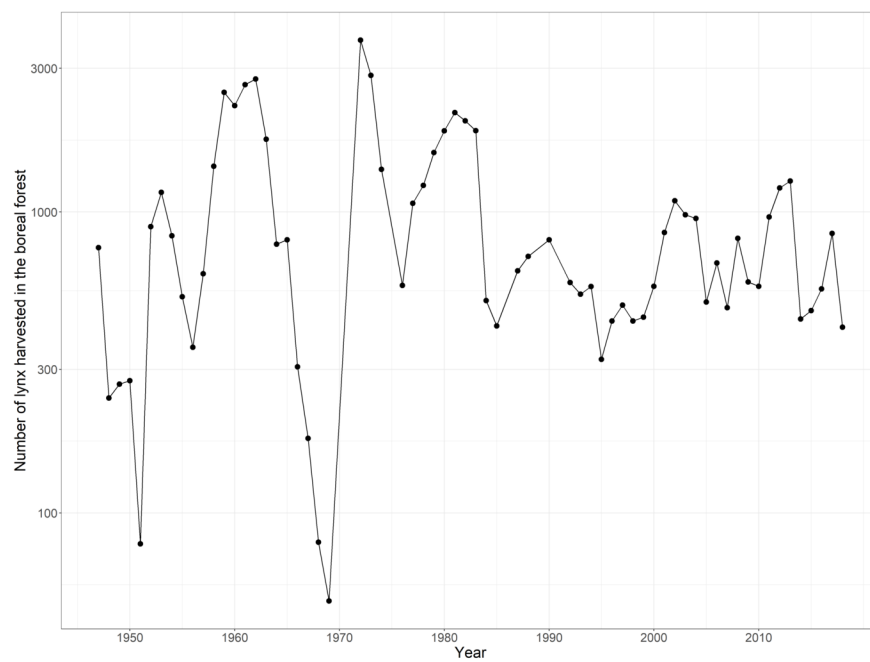
Figure S5. Number of Canada lynx harvested in the boreal forest of Ontario from 1948 to 2018. Records used to estimate the southern range at the southern boundary of the boreal forest were removed.