Range dynamics of two closely related felids

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Abstract

Range dynamics of two closely related felids

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Species ranges are changing and the rate at which the climate is warming is faster than anything previously seen in the past, consequently species will need to adapt quickly, track the climate or perish. Cold adapted terrestrial species are the most vulnerable, because they are limited by the availability of land at the cold edge of their range. This means that many alpine, boreal and polar species essentially have nowhere to go as the climate warms. Habitat generalists are widely distributed across the globe and are highly adaptable to anthropogenic change. Our future biodiversity may only consist of several habitat generalists. The Canada lynx (*Lynx canadensis*) is a boreal species that has limited range expansion potential at the cold end of its range and its range has already contracted by 40%. The lynx has nowhere to go as climate warming progresses in this current century. Therefore, understanding the causes of its range contraction could enlighten us on conservation and management strategies that we might undertake as climate warms. My analyses indicated that the Canada lynx seems to have tracked the habitat that it is adapted to in more northern homogenous boreal forests and the bobcat (*Lynx rufus*), a habitat generalist, has simply replaced it in the south.

Keywords: Range change, Connectivity, Competition, Anthropogenic Change, *Lynx canadensis*, *Lynx rufus*

Preface

I have written my dissertation in manuscript format, since my chapters have been published or submitted for publication. Chapter 3 will be submitted to Ecography, chapter 4 was published in PLoS One, chapter 5 was published in Ecology and Evolution and chapter 6 was accepted for publication in FACETS. Each chapter was written in the style of its journal. All my research has been in collaboration with others; therefore, I have used the plural "we" where appropriate in my dissertation. I have indicated the names and roles of my collaborators on the title page of each chapter. I have obtained permission to reprint articles from the copyright holders (Appendix A).

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Chapter 1: Introduction

The geographical area where a species persists is its range (MacArthur 1972) and is essentially the projection of its ecological niche in space (Sexton *et al.* 2009). In this bounded area, a species' niche requirements are met; accordingly, birth rate outweighs death rate and the population sustains itself in perpetuity unless modified (Kirkpatrick and Barton 1997). The boundaries of this range can be limited by large physical barriers such as deserts, mountains, and waterbodies, that a species cannot disperse across (Gaston 2009). Therefore, a species' intrinsic traits determine its dispersal ability and consequently plays an important role in limiting a species range in this context (Holt 2003).

However, in many cases the reason why a species' range does not extend over certain areas is not quite as simple. Within a species' range, density and occupancy generally decline towards the range limit (Hengeveld and Haeck 1982, Brown 1984, Gaston 2003, Gilman 2006, Yakimowski and Eckert 2007). These less apparent barriers in the form of abiotic gradients impose restrictions by gradually reducing birth rate and/or increasing death rates towards the periphery (Gaston 2009). For example, temperature and moisture are important abiotic limiting factors and impose both latitudinal and elevational gradients that mold the range of many species and this forms many unique species assemblages (Whittaker 1962). However, biotic interactions such as competition, predation, mutualism and parasitism can also limit a species' range, since populations will be influenced by both negative and positive interactions (Briers 2003, Holt and Barfield 2009, Stanton-Geddes and Anderson 2011). It is suggested that the cold end of a species range is limited by abiotic factors, while at the warm end by biotic interactions (Darwin 1859, Dobzhansky 1950, Pianka 1970, MacArthur 1972, Cunningham *et al.* 2016,). Consequently, overriding spatial patterns in physical barriers, abiotic, and biotic interactions are responsible for generating all the interesting range patterns observed in nature.

Range change

Over the past century the range of many species has changed and has been attributed to anthropogenic change in the form of climate and land cover/use modification (Walther *et al.* 2002, Laliberte and Ripple 2004, Thomas 2010). In addition, many species have gone extinct due to anthropogenic change (Pounds *et al.* 2006). Unfortunately, species decline due to anthropogenic change is not easily detected and consequently there are many species that are currently undergoing significant change because of it but we cannot yet, directly see the repercussions (Thomas *et al.* 2006).

There are many ways in which the warming climate has impacted species ranges, for example by the reduction of the extent of sea ice (Derocher *et al.* 2004), decreased snow cover (Sultaire *et al.* 2016), increased variability of rainfall (Thuiller *et al.* 2006), the timing of seasons (Jenni and Kery 2003). Anthropogenic change in the form of land cover and land use modification has impacted the range of species by land clearing for logging (Smith *et al.* 2000), surface mining (Lacki *et al.* 2004), urban development (Scheffers and Paszkowski 2012), and agriculture (Calver and Dell 1998). The introduction of invasive species into new geographies has also changed the distribution of species into areas that were geographically isolated (Mooney and Cleland 2001).

Adapt or disperse

A species might locally adapt to the changing environment by broadly exploiting resources at the extremities of its niche (Sexton *et al.* 2017), by phenotypic plasticity (Nicotra *et al.* 2010, Valladares *et al.* 2014) and by evolving (Williams *et al.* 2008). However, the rate at which current conditions are changing may make it impossible for many species to adapt in these ways (Davis and Shaw 2001, Loarie *et al.* 2009). Another solution is a species can move to track the climate to areas that are within its bioclimatic niche (Visser 2008).

A species dispersal capability is limited by its physiology (Travis *et al.* 2013), its demography (Clark *et al.* 2001) and its behavior (Ehrlich 1961, Pusey 1987, Warren *et al.* 2001). For example, the range of some species might be dependent on density at the range periphery. In years where a population is flourishing, due to overpopulation in the core range, individuals will begin to occupy less suitable habitat at the periphery and individuals may also disperse and colonize unoccupied habitat (Travis *et al.* 1999). This density dependent dispersal might rescue disjoint populations (Brown and Kodric-Brown 1977) and may also ephemerally expand the range limit (Murray *et al.* 2008).

Nevertheless, the dispersal ability of a species is an important factor that limits a species range and is an essential intrinsic characteristic that may determine future biodiversity in this rapidly changing world (Bell and Gonzalez 2011, Schloss *et al.* 2012, Travis *et al.* 2013). Many species will go extinct because they cannot locally adapt, but even species that were once thought to be quite mobile might not be able to track changing environment due to how fast the climate is changing (Schloss *et al.* 2012). More adaptable species such vagile habitat generalist have a high capacity to overcome anthropogenic change (Baskin 1998). In fact, we are witnessing the homogenization of biodiversity across the globe, where habitat specialist species are being replaced by generalists (McKinney and Lockwood 1999).

Connectivity

When adaptation to local changes is not possible, dispersal is the only way forward; however, persistence not only depends on a species dispersal capability, but also on the degree to which the landscape promotes or hinders the dispersal of individuals (Fahrig and Merriam 1985, Fahrig and Paloheimo 1988). Large natural physical barriers such as mountains, oceans, lakes, and rivers can impede dispersal (Stebbins 1949, Steeves *et al.* 2003, Grant and Grant 2009). However, even though highly mobile species may be able to track the changing climate across these natural barriers, the addition of cities, highways, roads, crop lands, etc. can only hinder their mobility (Epps *et al.* 2006, Riley *et al.* 2006, Robillard *et al.* 2015). Eventually, animals will need to migrate across these highly modified landscapes to seek refuge poleward of their historical range. It is therefore necessary to understand the influence that anthropogenic barriers have on a species dispersal ability and consequently the impact of these barriers on the connectivity of a population.

Available habitat

Even if a species can migrate across a complex landscape and reach potential areas of colonization, its establishment might not be possible due to restrictions imposed by its biophysical requirements (Grinnell 1917, MacArthur 1972) and interactions with other organisms (Silvertown 2004, Urban *et al.* 2012). The rate at which a species range will shift with climate also depends on whether newly opened habitat north of its range fits well within the multi-dimensional environmental requirements and resources that it needs to persist in the future (Hutchinson 1957, Hutchinson 1978).

Furthermore, suitable habitat might be found several hundreds of kilometers north of a species current range, but the environmental characteristics of the landscape between could be well outside of its niche breadth and dispersal through this environment could be impossible (Early *et al.* 2011). In this case the environment impedes or blocks dispersal and consequently the colonization of newly available habitat (McRae 2006, Wang and Bradburd 2014). Generalist species are distributed across a variety of climatic conditions and thus have a wide niche breadth and are more tolerant to climate change compared to specialist species that exploit a narrow niche breadth (Thuiller *et al.* 2005, Brown 1995). Due to their ability to cope in a broad variety of habitats, generalist species are more likely to succeed in tracking climate change and colonizing newly available habitat (Warren *et al.* 2001, Clavel *et al.* 2010).

Biotic interactions

Species redistribution is leading to increased sympatry (Gilman *et al.* 2010). Interactions in these areas of overlap may hinder a species ability to track anthropogenic change in the form of competition or predation (Urban *et al.* 2012, HilleRisLambers *et al.* 2013). In addition, similar species may hybridize and may create more adaptable species (Hoffmann and Sgro 2011), but this may also threaten native species by introgression hybridization (Chunco 2014). Consequently, the rate at which a species' range will shift with climate not only depends on its dispersal ability, connectivity and its fundamental niche requirements, but also on species interactions (Gilman *et al.* 2010, Boulangeat *et al.* 2012, Svenning *et al.* 2014).

Competition, predation and symbiosis impose further restrictions or advantages to species tracking climate change (Connell 1961, Silander and Antonovics 1982, Urban *et al.* 2012). The requirements of the fundamental niche of a species might be met, but biotic interactions will further shape the area that species might colonize (Hutchinson 1957). A species realized niche might be a small fraction of the area where environmental conditions fit within a species fundamental niche requirement (Connell 1961). As species track climate, species with overlapping niche breadths may meet. Phylogenetic niche conservatism theory tells us that in areas of contact, species will conserve their ancestral traits, and this will result in interspecific competition and eventual competitive exclusion of the lesser competitor (Violle *et al.* 2011). On the other hand, coexistence of closely related species does happen in nature (Rydin and Barber 2001, Pigot *et al.* 2016). A likely mechanism for coexistence is spatial segregation (MacArthur 1958) and niche partitioning (Chase and Leibold 2003). In other words, to avoid competition, closely related species that exploit similar niches will evade each other in space or time or exploit completely different parts of their niche breadth.

Nowhere to go

Many species that have ranges that are restricted by available land near the poles will be limited in their ability to track climate because they are essentially blocked by the availability of space to move to higher latitudes or elevations (Kerr and Packer 1998). Therefore, many unique alpine, polar and boreal specialists will eventually perish unless they somehow adapt to much warmer conditions and adapt to new biotic interactions. It is generally thought that the range of species is limited at the cold end of their range by abiotic factors such as temperature and limited at the warm end of their range by biotic interactions such as competition (Darwin 1859, Dobzhansky 1950, Pianka 1970, MacArthur 1972, Cunningham *et al.* 2016). Consequently, cold adapted terrestrial species are already limited at the warm edge of their range by biotic interactions, and with the warming climate. These interactions will only intensify and further limit their range while at the same time they are tracking climate to colder regions but will eventually have nowhere to go (Kerr and Packer 1998). Understanding the causes of these range dynamics of these cold adapted species is important in making better predictions and consequently making better informed decisions for species management and conservation in this century, since anthropogenic change is not decelerating.

Causes of northward range contraction

Disentangling the cause of range contraction is important in helping us further manage and conserve unique cold adapted species that essentially have nowhere to go as the climate continues to warm (Kerr and Packer 1998). Unfortunately, the velocity at which climate is changing may make it impossible for many less adaptable and mobile species to adapt or even track the changing climate (Davis and Shaw 2001, Loarie *et al.* 2009). If we can disentangle the drivers of range change than we can make better predictions on how different anthropogenic change scenarios will play out. We would then better understand the degree to which climate, land cover and biotic interactions have on the range dynamics of many species. Therefore, a better understanding what factors are responsible for shaping the historical and current range of species will essentially help us make better informed decisions for management and conservation purposes for cold adapted species that are tracking climate, in many cases, towards a dead end.

Thesis Objectives

The general purpose of my thesis is to further our understanding of the causes of range dynamics of a unique cold adapted species the Canada lynx (*Lynx canadensis*) in the face of anthropogenic change and invading competitors. To do so I have investigated the following research questions:

- What drivers best explain the southern range dynamic of the Canada lynx?
- How is the range of a potential competitor, the bobcat, expanding northward?
- Is there evidence of competition in areas of range overlap?

Thesis Structure

My thesis is split into 5 main chapters, of which chapters 2, 3, 5 and 6 are directly associated to the main objectives. In chapter 2, I reviewed what factors are associated with the southern range contraction of the Canada lynx. In chapter 3, I investigated historical patterns of trapline occupancy of lynx over 6 decades in the southern range periphery in Ontario, Canada. I tested several hypotheses that might explain the observed range dynamics of the Canada lynx. I devoted chapter 4 to testing different methods that are used in chapter 5. More specifically, I investigated the differences between two methods that are commonly used to simulate movement between populations or individuals across a landscape and investigated how spatial and thematic aggregation influence both methods. In chapter 5, I applied what I learned about simulating gene flow in the previous chapter by investigating the range expansion of bobcats in the Great Lakes Region. I tested several hypotheses of connectivity and quantified the influence of landscape features on bobcat gene flow. In chapter 6, I investigated more closely an area in northeastern Ontario where bobcats and Canada lynx are both commonly found. I determined whether both species occurred together and whether they used the same habitat. Finally, chapter 7 was devoted to a synthesis of my results in the light of the information gathered in previous chapters.

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Chapter 2: Causes of the southern range contraction of the Canada lynx

Abstract

The range of the Canada lynx (*Lynx canadensis*) has contracted by 40% from its historical range and most of this contraction is northward, therefore it is the perfect species to study southern range contraction. As the climate warms the range of the lynx will only decrease, because northward expansion is limited by the tree line and the Arctic ocean. Trapping, habitat loss, loss of connectivity and competition have contributed to this range reduction, but the one major driver is the reduction of snowshoe hare in the southern periphery. Habitat loss have directly influenced the lynx, but indirect effects that negatively impact snowshoe hare are deleterious to the Canada lynx, because the lynx it almost exclusively preys on hares across its range. Snowshoe hare populations in the southern lynx range no longer reach numbers as they once did. Lower peaks in the snowshoe hare cycle decreases the probability of lynx dispersing into the periphery. As the climate warms, competitors will further be able to move into areas that once had deep snow and prey on snowshoe hare. In addition, the warming climate will change the snow regime and will likely result in a mismatch between snowshoe hare molt and season change. This will make the snowshoe hare more visible to predators and increase predation rates. The added predation can only result in the reduction of snowshoe hare, consequently the lynx will move northward to areas where the density of snowshoe hare matches their requirements. Consequently, the range contraction of the lynx can only be halted with sustainable snowshoe hare populations at the range periphery.

Introduction

The Canada lynx is an iconic, medium sized felid carnivore that largely resides in the boreal forest of North America (Poole 2003). The majority of its range is found in the boreal forests of Canada and Alaska, USA (Figure 2.1). The lynx is deemed a habitat specialist because it almost exclusively preys on snowshoe hare (O'Donoghue *et al.* 1998). Consequently, its population dynamics are highly coupled to the 8-11 year population cycle of the snowshoe hare density; mirroring it with a 1-2 year delay (Poole 2003). It has been estimated that over the past century the Canada lynx range has contracted by 40% (Laliberte and Ripple 2004). In fact, the lynx once occurred in 24 US States (McKelvey 2000), but now only occurs in Colorado, Idaho, Maine, Minnesota, Montana, Washington and Wyoming (US Fish and Wildlife Service 2017). Consequently, the lynx in the contiguous United States was designated as threatened (US Fish and Wildlife Service 2000). There is current debate about delisting the lynx in the US despite the tremendous reduction of its historical range.

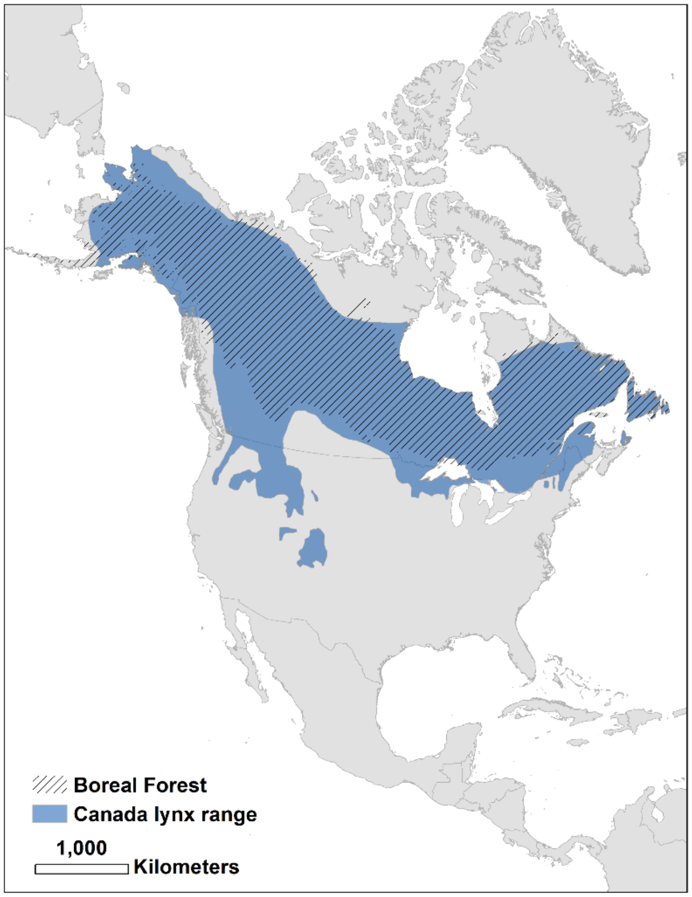

Figure 2.1. The range of the Canada lynx (Lynx canadensis. The range area was gathered from the International Union for Conservation of Nature (IUCN 2008). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/). The boreal forest layer was gathered from Natural Resources Canada (nrcan.gc.ca) and was developed by Brandt (2009).

In Canada, the lynx historically occurred in all provinces and territories and even recently has occupied 95% of its historic range (Poole 2003). However, it is designated as regionally Endangered in Nova Scotia (Parker 2001), New Brunswick (New Brunswick Endangered Species Regulation 2013) and is completely absent from Prince Edward Island (Poole 2003). The range of the lynx in British Columbia has been stable since the 1930s, but in Ontario its range has contracted north by 175 km from 1972 to 2010 (Koen *et al.* 2014). The northern range of the lynx has some expansion potential into Nunavut but is generally bounded by the tree line and the

Arctic Ocean (Poole 2003). With nowhere to expand to in the north, habitat for the Canada lynx will be limited in the future by continued encroachment of unsuitable habitat from the south. Consequently, the lynx is one of several boreal species that has nowhere to go as climate change progresses and is therefore an interesting study species to investigate aspects of southern range contraction.

The bottom up influence of snowshoe hare

The Canada lynx is heavily reliant on the snowshoe hare, consequently lynx are predominantly found in areas where snowshoe hare density is above 0.5 hare per hectare (Ward and Krebs 1985). In the southern periphery of the lynx range, snowshoe hare populations no longer reach high densities as they did in the past (Aubry *et al.* 2000, Hodges 2000, Murray 2000) and this most likely accounts for the current range contraction in the southern periphery (Poole 2003). After peak hare years in the core range, the Canada lynx is more likely to occur south of their range, because of density dependent dispersal into the southern range periphery (McKelvey *et al.* 2000, Murray *et al.* 2008). Consequently, the lower peaks in the snowshoe hare cycle decreases the likelihood of dispersal of the lynx into the southern periphery (Poole 2003). Southern populations may only be viable if they are well connected to boreal lynx population as part of a larger metapopulation (McKelvey *et al.* 2000, Schwartz *et al.* 2002).

Secondary factors influencing range change

In addition to lower peaks in snowshoe hare, the northward contraction of the southern range could have been caused by individual impacts or additive and interactive effects of habitat loss (Koehler 1990, Poole 2003, Kosterman *et al.* 2018), reduction of connectivity with northern populations (Aubry *et al.* 2000, Buskirk 2000, Walpole *et al.* 2012), trapping (Poole 2003), competition (Buskirk 2000, Boutin 2005, Murray *et al.* 2008), and climate change (Krebs 2010, Koen *et al.* 2014).

Land cover change

Habitat loss and loss of connectivity are also an important driver of range contraction of the Canada lynx (Koehler 1990, Poole 2003, Hornseth *et al.* 2014). At the southern range periphery, ideal habitat for lynx should have abundant and connected mature forest with intermediate amounts of small-diameter regenerating forest, as this provides an abundant temporally stable snowshoe hare population (Kosterman *et al.* 2018). For example, the lynx once occupied the US Great Lakes states but is now rarely seen there (McKelvey 2000, Poole 2003). Since 1836, open land increased from 12.3% to 41.3% due to land clearing for agriculture and urban development (Schulte *et al.* 2007). Forest complexity is now much lower, and the area occupied by coniferous forests has decreased (Schulte *et al.* 2007). Consequently, sparse accounts of the Canada lynx in the southern Great Lakes region is partly due to several centuries of land clearing for settlement, forestry and agricultural purposes (de Vos 1964, Poole 2003).

Trapping

The trapping of furbearers is a historical tradition in most of the range of the Canada lynx. In the past, over-harvest has led to the reduction and extirpation of many species in North America (de Vos 1964, Brander and Brooks 1973, Koehler and Aubry 1994). However, unregulated trapping is a thing of the past, as increased regulation followed historical population lows of many furbearer species that occurred in the 1930s and 1940s. Regulated lynx trapping occurs in Alaska, US, and most of Canada. Trapping the Canada lynx is prohibited however in the contiguous United States and the Canadian Maritimes provinces.

The lynx has a low-to-intermediate resiliency to trapping compared to other furbearers and harvest rates of the lynx should not surpass 40% of the pre-harvest population during the increasing phase of the hare cycle (Banci and Proulx 1999). Alternatively, when the snowshoe hare cycle is at a low, some researchers recommend a 3-year trapping restriction to assure that an adequate breeding population is present (Brand and Keith 1979), since the lynx that survive these years of scarcity will determine how fast the population will recover (Banci and Proulx 1999). If numbers are too low, recovery could be hampered despite abundant snowshoe hares (Poole 1994).

Competition

The introduction of novel competitors within the southern range periphery of the Canada lynx might also be responsible for the northward range contraction (Murray *et al.* 2008). Cougars (*Puma concolor*), bobcats (*Lynx rufus*) and fishers (*Pekania pennanti*) occur in the southern periphery and mortality of lynx by these competitors has been documented (Koehler *et al.* 1979, Aubry *et al.* 2000, Squires and Laurion 2000, McLellan *et al.* 2018). The coyote is found in both northern and southern lynx populations, however the coyote was not always present in many areas of the Canada lynx range prior to 1900 (de Vos 1964). The presence of the gray wolf (*Canis lupus*) limits the distribution of coyotes (*Canis latrans*) on the landscape by interference competition (Miller *et al.* 2012). Wolves generally rely on larger prey and are at much lower density, consequently their impact on the snowshoe hare population is low enough that apparent competition with lynx is unlikely (Ripples *et al.* 2011). Therefore, the elimination and extinction of the gray wolf in the temperate zone of its distribution in North America may have caused the invasion of coyotes, a subsequent reduction of the hare population, and consequent impacts on the lynx (Ripple *et al.* 2011).

The range of the fisher has always overlapped a significant part of the southern range of the Canada lynx and their northward range contractions are quite similar (Laliberte and Ripples 2004). However, after its period of very low abundance across north America prior to the 1970s (Powell 1982), the fisher seems to be returning naturally and also being reintroduced to many areas of its historical range in the south, but especially in central and eastern North America (Brander and Brooks 1973, Powell 1993, Buskirk and Powell 1994, Lewis *et al.* 2012, LaPoint *et al.* 2015). In contrast, the Canada lynx is not recolonizing these areas.

The bobcat a closely related competitor?

The bobcat and the Canada lynx are closely related carnivore species and their ranges overlap in 3 areas in North America (Figure 2.2). The potential for competition has been of great debate (Parker *et al.* 1983, Hoving *et al.* 2003, Peers *et al.* 2013, Gooliaff and Hodges 2018, Gooliaff *et al.* 2018). A recent study showed that the bobcat and Canada lynx selected similar habitat at a fine scale, however their home ranges never overlapped, and this suggested that competition at higher orders has low potential (Morin *et al.* 2019). In British Columbia, Canada, the ranges of the lynx and bobcat appear not to have changed since 1935, and there is no evidence of competition (Gooliaff and Hodges 2018). However, Scully *et al.* (2018) found that the Canada lynx avoided areas when bobcats were present and suggested that the warming climate and eventually much shallower snow may result in the isolation of lynx habitat, which may increase competition potential between these species. In an earlier study, Parker *et al.* (1983) found evidence of range expansion of the bobcat into former lynx habitat in Cape Breton, Nova Scotia. They did not find any evidence of interaction between these species but indicated that decreasing snow depth promoted this invasion.

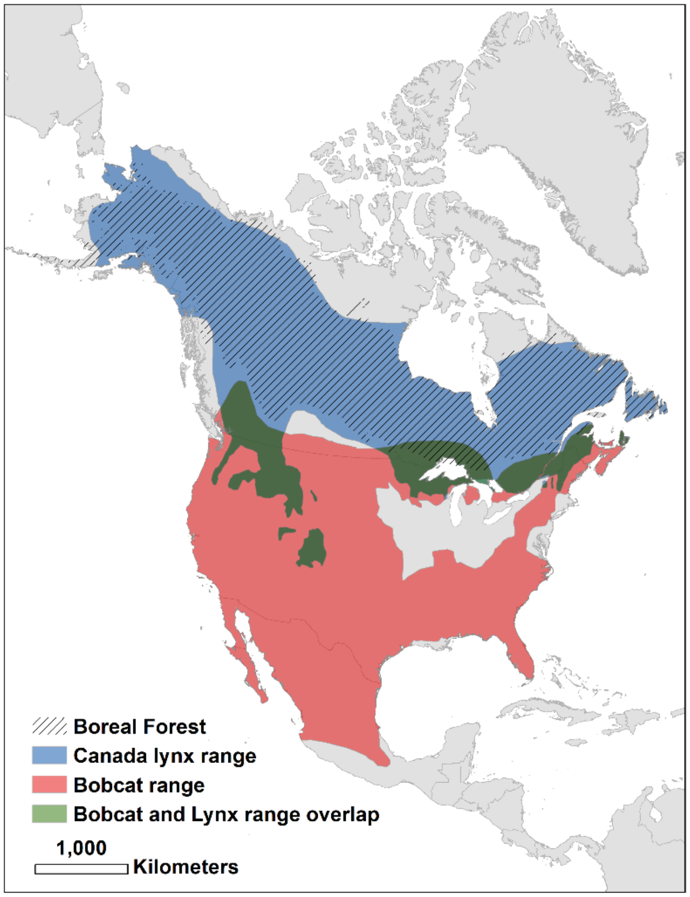

Figure 2.2. The range of the bobcat (Lynx rufus) and the Canada lynx (Lynx canadensis). Range areas were gathered from the International Union for Conservation of Nature (IUCN 2008). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/). The boreal forest layer was gathered from Natural Resources Canada (nrcan.gc.ca) and was developed by Brandt (2009).

In many other cases snow depth and snow hardness have been suggested to be important limiting factors for the bobcat, essentially limiting its invasion into lynx territory (Marston 1942, McCord 1974, Parker *et al.* 1983, Hoving *et al.* 2003, Morin *et al.* In Press). Conversely, bobcat generally occupies areas in North America that have shallow or no snow (Nowak 1999). The lynx has much larger feet than bobcat and have a competitive advantage in catching prey in deep snow (Larivière and Walton 1997, Nowak 1999, Anderson and Lovallo 2003). In fact, because of its large paws, the lynx can support at least twice the amount of weight compared to the bobcat at the same sinking depth (Parker *et al.* 1983). A broad-scale continental analysis suggested that the lynx and the bobcat might compete for resources (Peers *et al.* 2013). In sympatry, lynx in the study exploited a narrower bioclimatic niche whereas bobcats broadened their niche.

The potential for competition between these species can also be determined by looking at the theoretical implications of the hierarchical nature of habitat selection (Johnson 1980). Morin *et al.* (2019) reviewed whether there is any evidence of potential for competition between these two species. They tabulated habitat selection of each species for all Johnson orders of selection. To see if they overlapped, they looked at selection within the entire range of both species (1st Johnson order) to selection all the way down to the procurement of specific resources (4th Johnson order). Their reasoning was that if competition originates at lower orders of habitat selection, then theoretically competition is possible if the home ranges of the species overlapped. However, so far, no study has shown overlap and in addition both species also selected different resources at higher Johnson orders (coarser scale). Morin (2019) concluded that because habitat selection is conditional on higher orders of selection, then this would indicate that the potential competition between these species is less likely than previously thought.

Climate change and snow depth

The impact of climate change on the Canada lynx seems to be indirectly through its main food source the snowshoe hare. The timing between molt and season change for snowshoe hare is important in decreasing predation rates (Zimova *et al.* 2016). Also, the warming climate will change the snow regime, and this could increase predation rates, consequently this would reduce the amplitude of the hare cycle (Krebs 2010). Climate change will also open formerly inhospitable habitat to new species in the lynx range. The bobcat has smaller feet than the Canada lynx and this might be one factor that has impeded the bobcat from invading Canada lynx territory in the past (Marston 1942, McCord 1974, Parker *et al.* 1983). However, since the climate is warming, and snow depths across the southern periphery of the lynx range are shallower, bobcat are no longer hindered by snow. In fact, Parker *et al.* (1983) found that after several years of low snow, bobcats invaded the lowlands of Cape Breton while lynx had eventually left the area.

Conclusion

Anthropogenic change has many direct impacts on Canada lynx, but the indirect effects on snowshoe hare are likely more important, since the population dynamics of Canada lynx is highly coupled to that of the snowshoe hare. Consequently, the extent of the lynx southern range is primarily driven by the density of snowshoe hare. Competition may also pose a threat to the lynx in its southern range, but not by direct confrontation but in the form of competitive exclusion. As the climate warms, competitors will further be able to move into areas that once had deep snow and prey on snowshoe hare. The added predation can only result in the reduction of snowshoe hare, consequently the lynx will move northward to areas where the density of snowshoe hare matches their requirements. Indirect impacts through snowshoe hare might be important for understanding the range contraction of the lynx (Murray *et al.* 2008). In summary, the habitat specialist nature of the Canada lynx and the considerable range contraction it has undergone in the past century make it a suitable species to study causes of southern range contraction in the context of anthropogenic change.

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Chapter 3: Southern range dynamics of Canada lynx over 66 years

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A version of this chapter will be submitted to Ecography for publication

Contributions: RRM and JB conceived and designed the study; RRM analyzed the data and wrote the manuscript; JB critically reviewed the manuscript.

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 2010-2014. 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.

Keywords: Canada lynx, Great Lakes Region, harvest records, *Lynx canadensis*, range dynamics, spatiotemporal,

Introduction

Over the past century the range of many species has changed, and this has been attributed to climate change and land cover modification (Thomas 2010, Laliberte and Ripple 2004, Walther et al 2002). A species can deal with these changes by broadly 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 evolution (Williams *et al.* 2008). However, the rate at which current conditions are changing may 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 the bioclimatic niche they evolved in (Visser 2008). Therefore, the dispersal ability of species will be an essential intrinsic characteristic that may determine future biodiversity in this rapidly changing world (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 essentially blocked by the availability of space to move to higher latitudes and will have nowhere to go (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 warm range of these cold adapted species has been changing would help us in making better informed decisions for species management and conservation, 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 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 and mirrors it with a 1-2 year delay (Poole 2003). It has been estimated that over the past centuries 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). Thus far, this earlier range contraction has not been attributed to change in climate.

Canada lynx are predominantly found in areas where snowshoe hare density is above 0.5 hare per hectare (Ward and Krebs 1985, Hodges 2000, Ruggiero *et al.* 2000, Squires and Ruggiero 2007, Maletzke *et al.* 2008, Zahratka and Shenk 2008, Hodges *et al.* 2009, Berg *et al.* 2012, Ivan *et al.* 2014). In the southern periphery of the lynx range, snowshoe 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). After peak hare years in the core range, Canada lynx are more likely to occur south of their range, because of density-dependent dispersal into the southern range periphery (McKelvey et al 2000, Murray *et al.* 2008). Consequently, the lower peaks in the snowshoe hare cycle might decrease the likelihood of dispersal of lynx into the southern periphery (Poole 2003). This is further amplified with decreasing connectivity to northern populations (Ruggiero *et al.* 2000, Buskirk 2000, Walpole *et al.* 2012).

The warming climate will 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). The warming climate will change the snow regime, and this could increase snowshoe hare predation rates by increasing the rate of mismatch between snowshoe hare molt and season change. Consequently, predators will have a much easier time finding snowshoe hares as the climate warms and this would also reduce the amplitude of the hare cycle and likely that of the lynx (Krebs 2010).

Climate change will also open formerly inhospitable habitat to new species in the lynx range. The bobcat (*Lynx rufus*) and the coyote (*Canis latrans*) have smaller feet than the Canada lynx and cannot support as much weight as the 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, these competitors are no longer as hindered by snow and this may increase 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.

The lynx once occurred in 24 US 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 this tremendous range contraction, its protection status is being debated and it might be removed from the list of endangered species in the United States. The lynx was originally listed because of habitat loss due to forestry practices. The current consensus is that habitat loss was mitigated and lynx populations in the US are doing much better. The hope is that after its protection status is removed forest management guidance will be maintained. In Canada, the lynx occurred in all provinces and territories and currently 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 the 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).

The purpose of this study was to estimate the past extent of the Canada lynx southern range using harvest records and then to determine whether the spatial-temporal patterns can be attributed to snowshoe hare and boreal lynx population dynamics, connectivity, climate, land use and competition. We predicted that years with fewer lynx in the boreal forest, led to a reduction of the extent of the southern Canada lynx range. We also predicted that areas with high human disturbance, shallow snow, presence of competitors, and with low connectivity to boreal lynx populations are 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 outside of the boreal forest where lynx occurred at least once between 1948-2014 in Ontario, Canada (Figure 3.1). 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 2 distinct southern range zones in Ontario separated by Lake Superior: the western and the eastern zones. We further split the eastern zone into a northeast and southeast zone. We used these zones to illustrate regional trends in range change, since these zones had very different spatial and temporal patterns. Both northern zones (west and northeast) were at most 100 km south of the southern edge of the boreal forest, whereas the southeastern zone was more than 100 km south.

The southern lynx range in Ontario is 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).

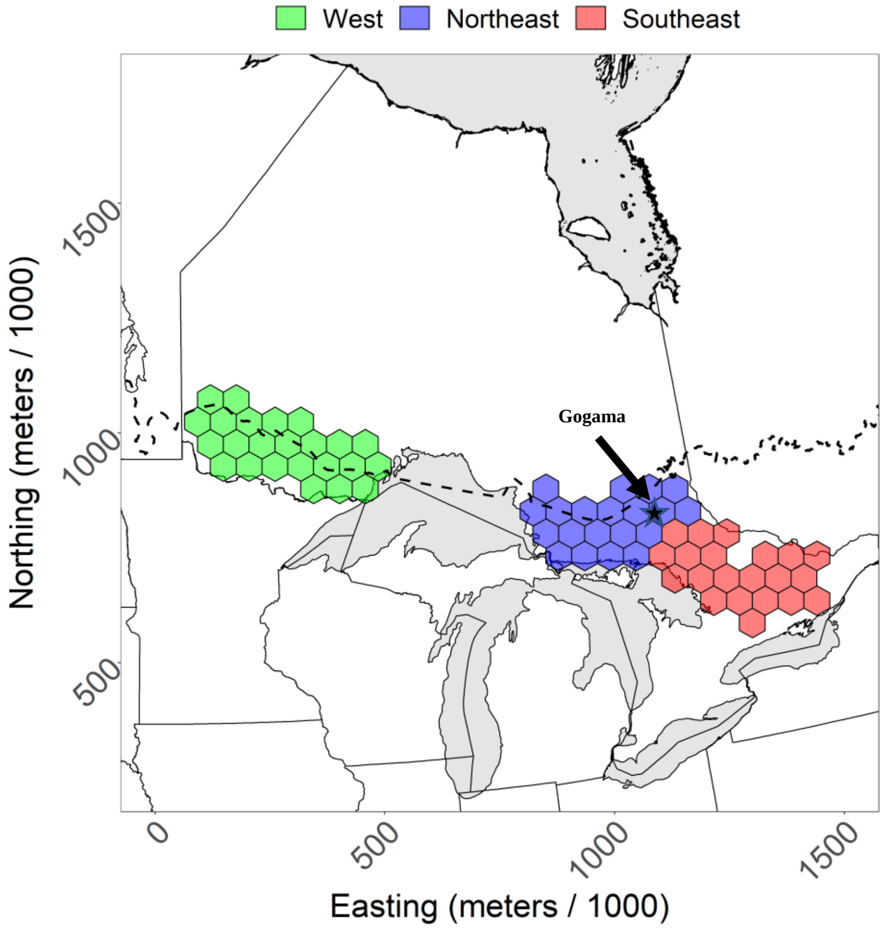

Figure 3.1. Sampling units in the southern Canada lynx range in Ontario, Canada used to estimate the probability of harvesting a lynx between 1948-2014. The black line is the southern limit of the boreal forest by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).

Harvest records

Long term spatial data on terrestrial species are quite rare. Fortunately, wildlife agencies track the number of furbearers harvested each year. In addition, fur traders (*e.g.* Hudson's Bay Company and North West Company) compile similar records. These records contain important information that could 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).

Some organizations have been compiling fur-returns before the 19th century (*e.g.*, The Hudson's Bay Company). With these records, ecologists have attempted to answer fundamental questions in ecology in the past (Krebs *et al.* 1995; Keith 1963; Elton 1942; Elton and Nicholson 1942). There are, however, some issues with using fur returns. Trapping effort must be accounted for or perceived population dynamics could simply be a signal of trapping effort (DeVink *et al.* 2011, Dorendorf *et al.* 2016) and generally the location of where animals were trapped is only available at a very 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 3.2). The 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 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.

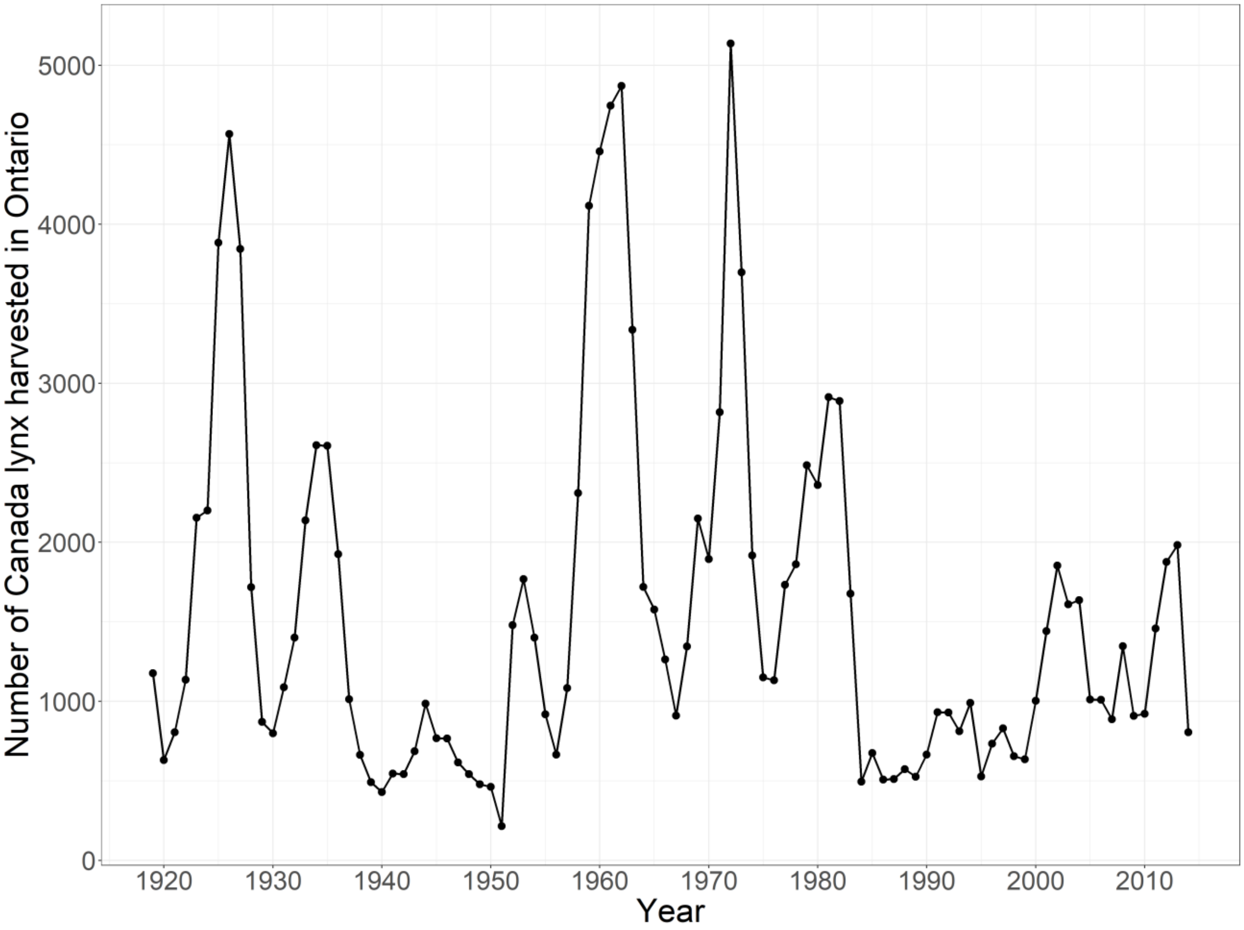

Figure 3.2. Number of Canada lynx harvested in Ontario, Canada between 1919-2014. Values earlier than 1947 were from Novak (1987a and 1987b). Later values were aggregated from the Ontario fur returns that were used in this study.

Spatial and temporal coverage

Boundaries of trapping units changed occasionally due to regulation changes. Therefore, we divided the southern Canada lynx range into 65 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 2014. We assigned each trapping units to the hexagon that its centroid fell into. All the information in each trapping record was then aggregated to the sampling unit. 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 62 years to only 20 years for the 67 years period between 1947-2014.

Due to this 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 2014, because the trapline system was not completed yet in 1947 and therefore had limited spatial coverage. Also, interpolating these cases was not possible, since we did not have information from 1946. This is because traplines in Ontario were yet completely established in 1947. We further restricted our analysis to sampling units that had at least one lynx that was harvested from 1948 to 2014. Next, we restricted our analysis to sampling units that did not have more than 5 years of consecutive missing data. We also restricted our analysis to sampling units that had at least 85% temporal coverage (57/66) or at most 10 years of missing records between 1948-2014. Finally, we removed sampling units that contained on average less than 1000 km^2 of trapping unit surface area between 1948-2014. 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).

Estimating the spatial and temporal range

We used a Hierarchical Generalized Additive Models to estimate the probability of harvesting a Canada lynx within a sampling unit across space and time. 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 (Marra *et al.* 2012, Poggio et al 2012, 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 in R 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 2014.

Trapping effort covariates

We investigated 3 types of effort measures related to 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 occupied 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 pattern 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 weren't 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.

We calculated the average price of lynx pelts that originated from Ontario using the fur-return summaries from a variety of sources. We gather 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 2011 were missing. Therefore, we used summaries provided by the Fur Institute of Canada for 2010-2014 (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 (http://www5.statcan.gc.ca; CANSIM Table 326-0021). For each year we multiplied the average pelt price by the 2016 CPI and divided these values by the CPI of their appropriate year. This adjusted the average pelt prices to 2016 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 1948-2014. 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.

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.

For our hare density time series, we gathered proxy hare density data from The Ontario Ministry of Natural Resources and Forestry (OMNRF Unpublished). Long term monitoring of hare populations is undertaken through an array of lagomorph pellet count plots in several locations across the province (Bendell and Young 1995). The longest running snowshoe hare population monitoring is in Gogama, Ontario (Figure 3.1); this study has been active since 1986. 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 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. 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 2014. 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 model fitting in R version 5.5.1 (R Core Team 2014) using the automap (Hiemstra and Hiemstra 2013), mgcv (Woods 2011), ppcor (Kim 2015), sp (Pebesma and Bivand 2005), raster (Hijmans and van Etten 2014), rgdal (Bivand *et al.* 2018), rgeos (Bivand and Rundel, 2013), tseries (Trapletti and Hornik 2019), and spdep (Bivand and Wong 2018) packages. 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 was a model that included the log transformed total number of furbearers harvested and a thin plate smoother on the spatial coordinates (Table 3.1). This model was 18.982 AIC units lower than all other models and its AIC_w was 1.000. The spatiotemporal effort model had an adjusted R^2 of 0.58 and a deviance explained of 53.6%.

Table 3.1. 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 1948-2014 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 Deviance Explained	R^2	AIC	ΔAIC	ω
1	Total Harvest	TP	1465.418	0.536	0.580	2739.017	0.000	1.000
2	Average Total Harvest	TP	1476.873	0.533	0.577	2758.000	18.982	0.000
3	Total harvested Density	TP	1486.849	0.531	0.576	2772.485	33.468	0.000
4	Marten Harvest Density	TP	1489.914	0.531	0.577	2777.286	38.268	0.000
5	Marten Harvest	TP	1496.375	0.529	0.575	2788.642	49.625	0.000
6	Marten Average Harvest	TP	1498.494	0.529	0.574	2791.705	52.688	0.000
7	Total Harvest	MRF	1556.322	0.582	0.603	2907.767	168.750	0.000
8	Average Total Harvest	MRF	1562.684	0.585	0.605	2913.063	174.046	0.000
9	Total harvested Density	MRF	1567.634	0.584	0.606	2918.064	179.046	0.000
10	Marten Harvest Density	MRF	1558.504	0.581	0.604	2920.023	181.005	0.000
11	Marten Average Harvest	MRF	1562.199	0.583	0.605	2925.365	186.348	0.000
12	Marten Harvest	MRF	1562.051	0.582	0.604	2925.541	186.524	0.000

Other than the total number of furbearers harvested, all 3 other effort related predictors followed a linear relationship (Figure 3.3). 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.

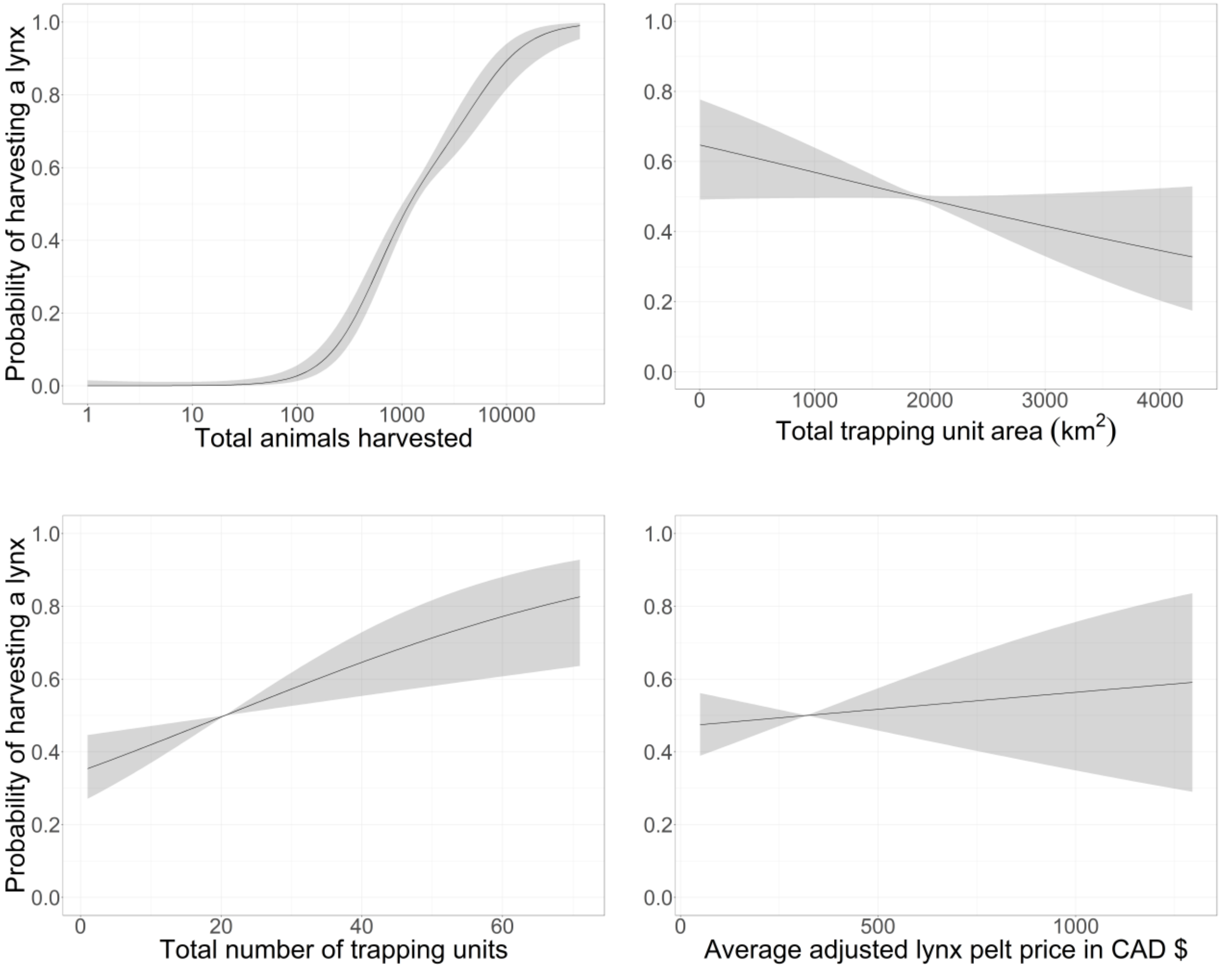

Figure 3.3. Effort covariates for predicting the probability of harvesting a Canada lynx between 1948 and 2014 across sampling units south of the boreal forest in Ontario, Canada.

The probability of harvesting a Canada lynx south of the boreal forest across Ontario changed through time (Figure 3.4). During the late 1940s and the early 1950s, the likelihood of harvesting of Canada lynx was at its lowest. However, in the mid-1960s the odds peaked across the southern range and even trapping units found in the southeast had a high probability. After this peak lynx period, it then became unlikely to harvest a lynx in the southeast and this pattern continued to 2014 (Figure 3.4).

The western range edge did not follow the same increase in range size as did the east during the mid-1960s. The western range did however peak a decade later in the mid-1970s. The western range then declined until the 2000s and increased slowly until 2014 to an overall probability of harvest higher than in previous years.

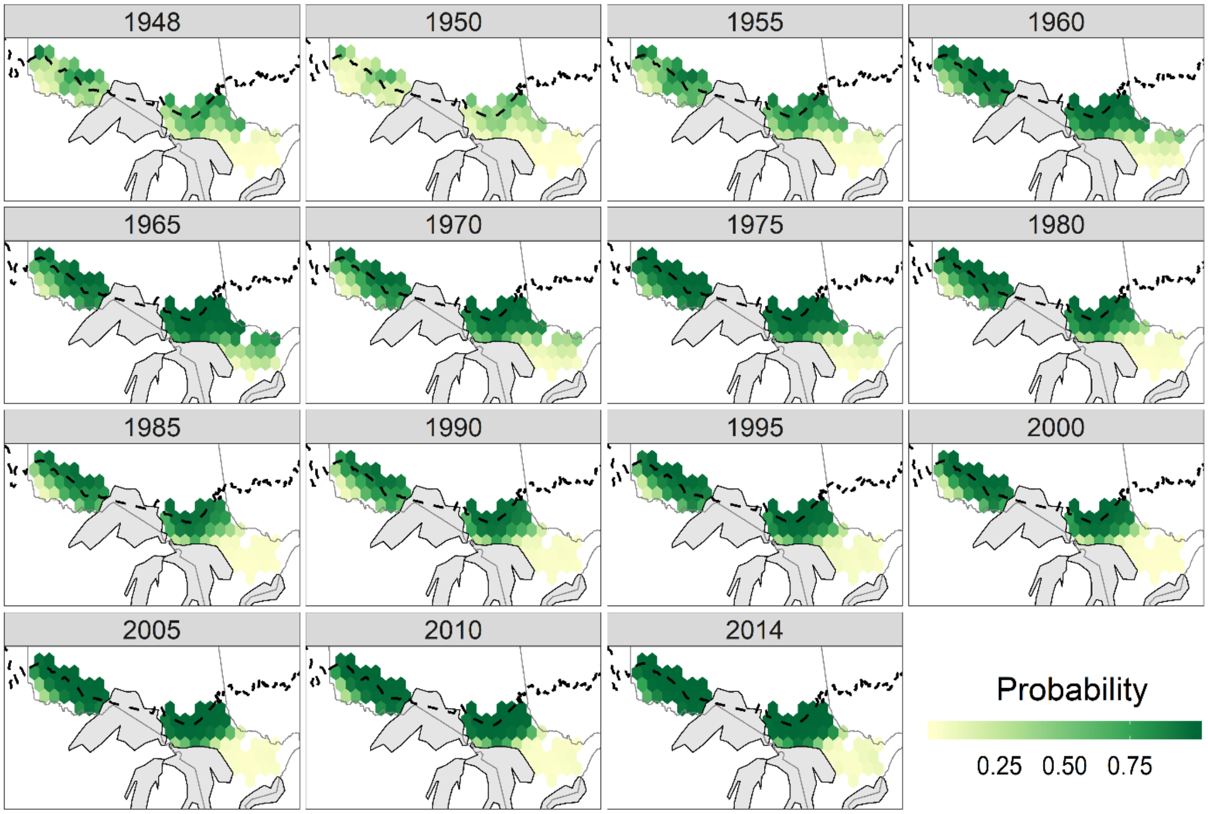

Figure 3.4. Spatial-temporal pattern of the probability of harvesting a Canada lynx south of the boreal forest in Ontario, Canada between 1948-2014. All years are available. The black line is

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/).

To get a better idea of the range dynamics, we calculated the area of the southern range of each zone for each year (Figure 3.5). 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.

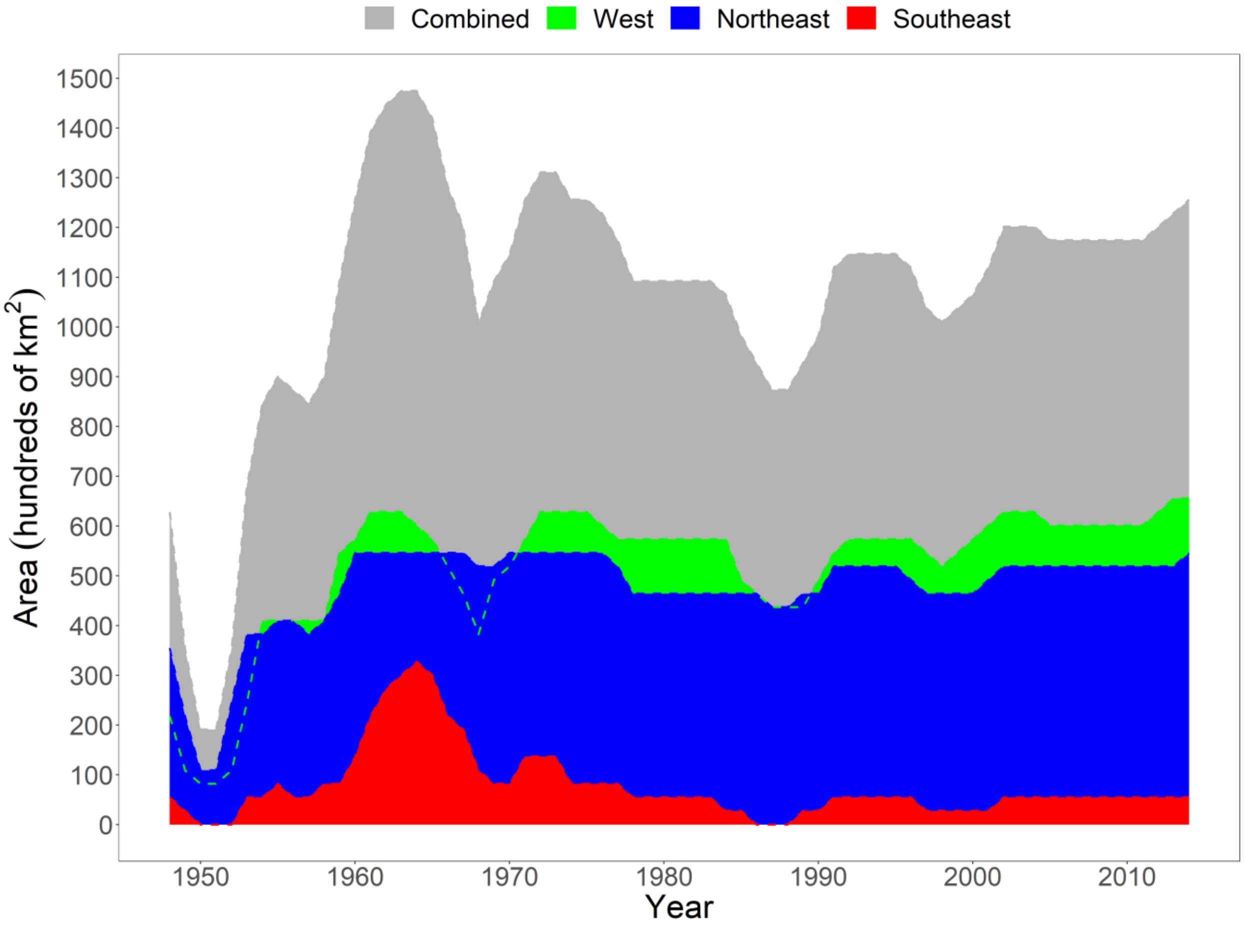

Figure 3.5. Area of the Canada lynx southern range in Ontario, Canada between 1948-2014. The maximum area of the west, northeast and southeast zone was 65,548.2, 54,623.5 and 57,354.7 km^2. The area was calculated by summing the area of the units (hexagons) that had a probability of harvesting a lynx over 0.5.

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 2014 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 followed similar patterns. However, from 1957 to 1964 the southeast zone increased from 5,462.3 to 32,774.1 km^2, which was a 6-fold increase and occupied most of the Lanark and Renfrew County just east of Ottawa (Figure S1). This increase was not as dramatic in the west and northeast, where there was only a 1.5- and 1.3-fold increase. Although, both northern 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.

From the late 1950s to 2014, the west and northeast 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 western zone reached its maximum area more recently in 2013 and 2014, whereas the northeast zone reached its maximum area multiple time in the periods 1960-1967 and 1970-1976. The southeastern 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 3.6). In the southeast zone, many sampling units are almost never within the range. In fact, on average these sampling units are only part of the range 9.0 years between 1948-2014. Whereas, the west and northeast zone are part of the range on average 53.0 and 58.3 years. The southwestern edge of sampling unit in these two northern zones are less frequently part of the southern lynx range.

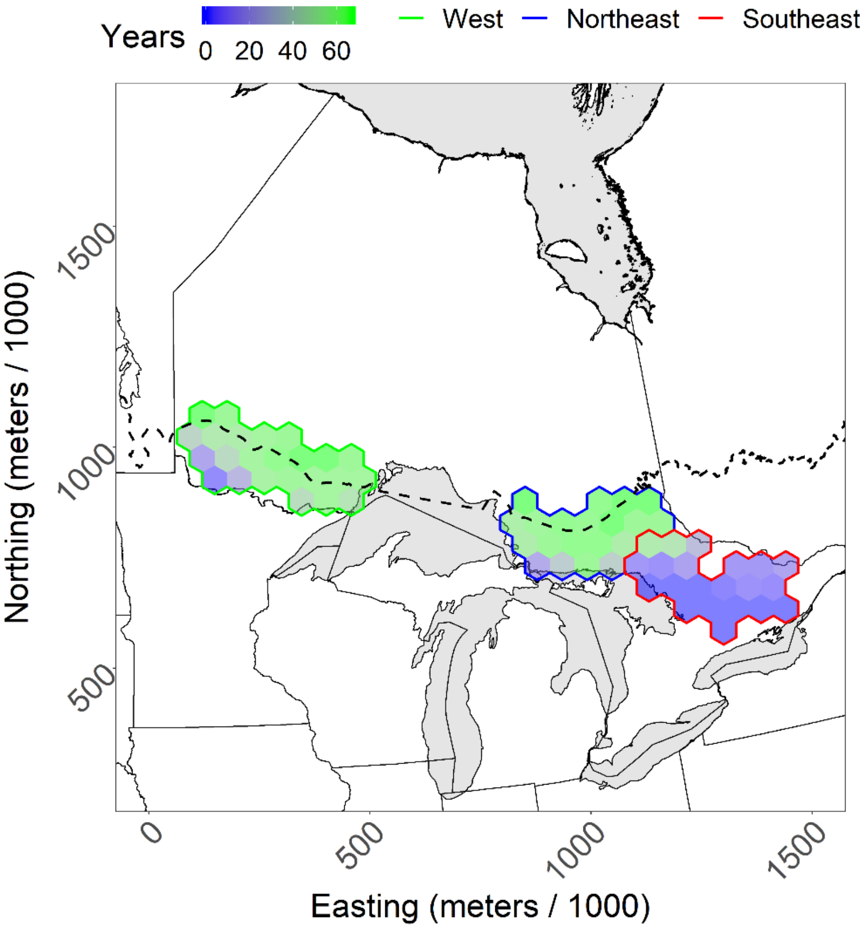

Figure 3.6. Frequency or number of years that each sampling unit was part of the southern Canada lynx range between 1948-2014 south of the boreal forest in Ontario, Canada. The black line is the boreal forest southern limit by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).

We predicted that undisturbed areas with deep snow, an absence of competitors, and close 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 3.2). 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 3.2); when the number of Canada lynx in the boreal forest increased, the area of southern range increased the following year.

Table 3.2. 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**		**Temporal**			
		Partial ρ	**Prob.**	**ρ**	**Lag**	**Prob.**	**Span**
Distance boreal forest	**-**	**-0.344**	0.006				
Distance nearest road	+	0.171	0.185				
Average annual SDI	**+**	**0.465**	0.000	0.104	1	1.000	1952-2014
Bobcat presence	-	0.008	0.953	-0.235	0	1.000	1948-2014
Coyote presence	-	-0.030	0.818	-0.337	0	0.167	1948-2014
Average hare pellets	+			0.361	2	1.000	1986-2014
Boreal lynx harvested	+			**0.461**	1	0.020	1948-2014

Discussion

In Ontario, Canada the southern range of the lynx has recovered from a dramatic decline in the late 1940s (Figure 3.5). However, it has never returned to its short-lived maxima across its entire southern range in the mid 1960s. More recently, it reached its maximum extent in the west and northeast zones. After the mid-1980s, the southern range varied less and from 2010 to 2014, seemed to be increasing. Consequently, we did not find any substantial range loss in more modern times as in the contiguous United States (Ruediger *et al.* 2000), and as in a previous analysis in the same geography (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, US (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 historic extent (Laliberte and Ripple 2004).

The extensive contraction in the early part of our analysis may have extended from 1938 to 1951 (Figure 3.2). 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). Consequently, lynx fur returns for each jurisdiction in Canada were an order of magnitude lower during this 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 3.5). The ranged peaked in 1963-1964 and lynx were being harvested more than 100 km south of the boreal forest in Lanark and Renfrew counties for almost 10 years (Figure S1). 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 3.2). Density dependent dispersal from the boreal forest likely drives the southern lynx range in the northern Great Lakes region. Consequently, southern populations are only maintained as part of a large metapopulation (Steury and Murray 2004, Murray *et al.* 2008). During peak years, individuals venture south and colonize subpar 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 S2), therefore lynx populations south were no longer being rescued. Unfortunately, we could not connect these patterns to snowshoe hare dynamics, since we did not have a large enough sample size and did not have any spatial replicated to detect it (Table 3.2). Though there is strong evidence that this should be the case (Aubry *et al.* 2000).

What immediately followed was a period of slow decline from 1970 to the late 1990s, where lynx appeared and quickly disappeared from Lanark and Renfrew counties and a few areas more north. 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 3.5). Our results probably differ because we were able to assess a longer time series (1972-2010 vs. 1948-2014) and we examined a much larger area.

While it seems that the range dynamics are mostly driven by boreal lynx population dynamics, we also found that areas that had deep winter snow were often found within the southern lynx range. However, this relationship does not vary temporally with the area of the southern lynx range (Table 3.2). 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.

Human disturbance in the form of roads and competition from bobcats and coyotes does not seem to have influenced the southern range of the Canada lynx in Ontario. There was a slight 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 3.2). Future research should investigate the spatiotemporal dynamics between lynx and coyote to further understand whether competition by coyote impacts lynx in the southern range. 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 here.

We can surmise as to what the southern range may have looked like between 1919-1948 by extrapolating backwards. We found that the southern range increased following the boreal lynx increase (Table 3.2). We know that lynx harvest from 1919 to 1940 was at similar levels as it was between 1967 to 1984 (Figure 3.2) and the southern range at this later time fluctuated between 90,000 and 130,000 km^2 (Figure 3.5). Therefore, the southern range could have also fluctuated by the same amount during this earlier period and may also have resembled it. This may mean that lynx were found in the Lanark and Renfrew counties during this earlier period. The southern lynx range between 1940 until 1948 likely resembled the slow decline between 1970-1990. However, in this earlier period, instead of eventually increasing, the lynx range crashed to its lowest point by 1950.

Conclusion

In 2014, the southern range of the Canada lynx in Ontario was at its saturation point in the west and northeast zone. Lynx may make an appearance in the Lanark and Renfrew counties, since this is what usually occurred in the past when the southern range was saturated in the north. Lynx were in fact rare occurrences in the southeast in the past and will likely always be rare in these areas that are over 100 kilometers from the boreal forest. The southern range in Ontario is strongly driven by the boreal lynx population dynamics and this may mean that occurrences of lynx south of the border are likely of a bygone era, since lynx in the boreal of Ontario do not reach high numbers as they once did. This is even more true given how average annual snow decreases southward across the border. The only hope for Canada lynx in the northern US Great Lakes states is likely protected area in Minnesota and the Upper Michigan Peninsula. These areas might temporally accommodate sporadic migrants during population peaks in the boreal forest. However, the distance between these protected areas and core lynx boreal habitat is only increasing, since the climate is warming, and the boreal tree line is moving northward. In addition, pathways that connect these peripheral populations are being altered by forestry operations. Unfortunately, this means that it will soon be quite unlikely to experience seeing these unique shy boreal creatures south of the Canadian border in the Great Lakes region.

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Supplemental Figures

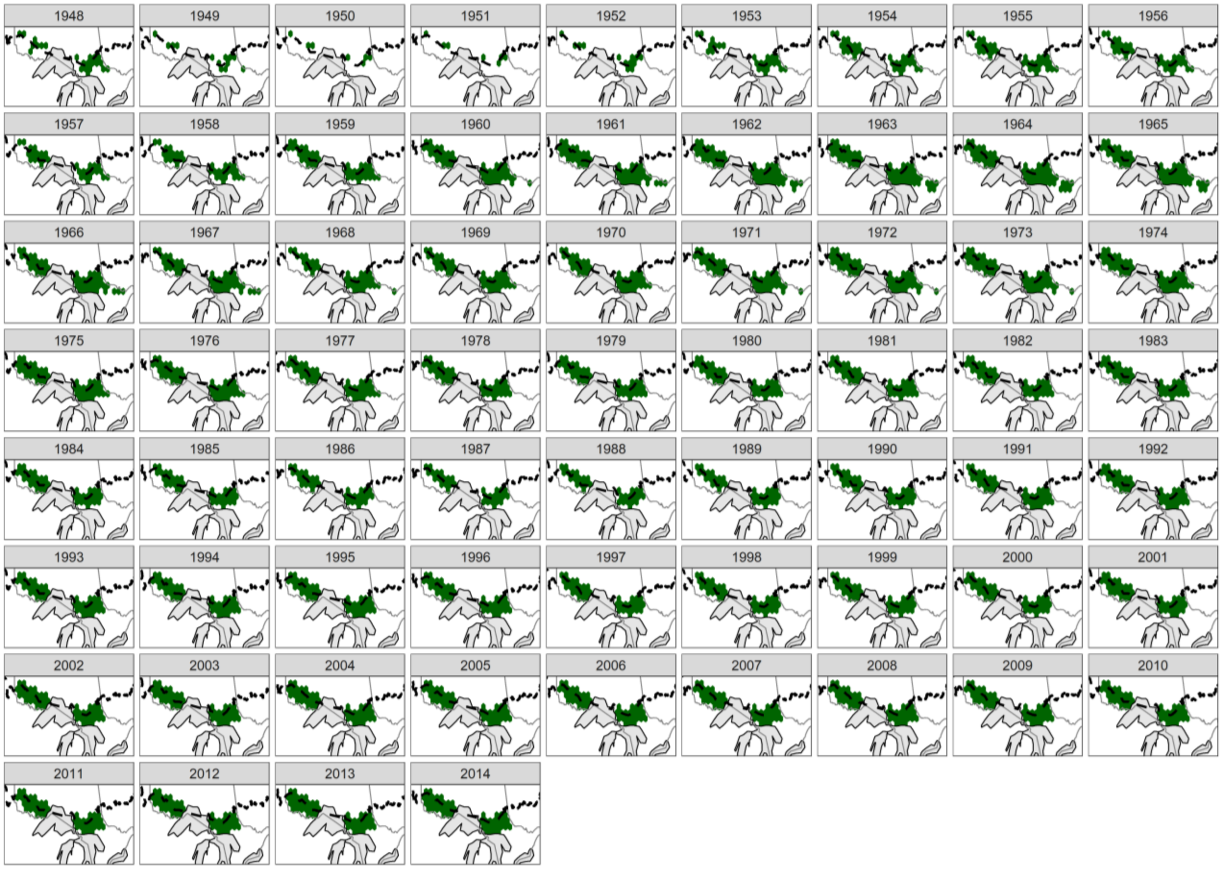

Figure S1. Southern range of the Canada lynx from 1948 to 2014 in Ontario, Canada. The range is a probability over 0.5 of catching a Canada lynx on a trapline within the same trapping conditions. The black line is the boreal forest southern limit by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).

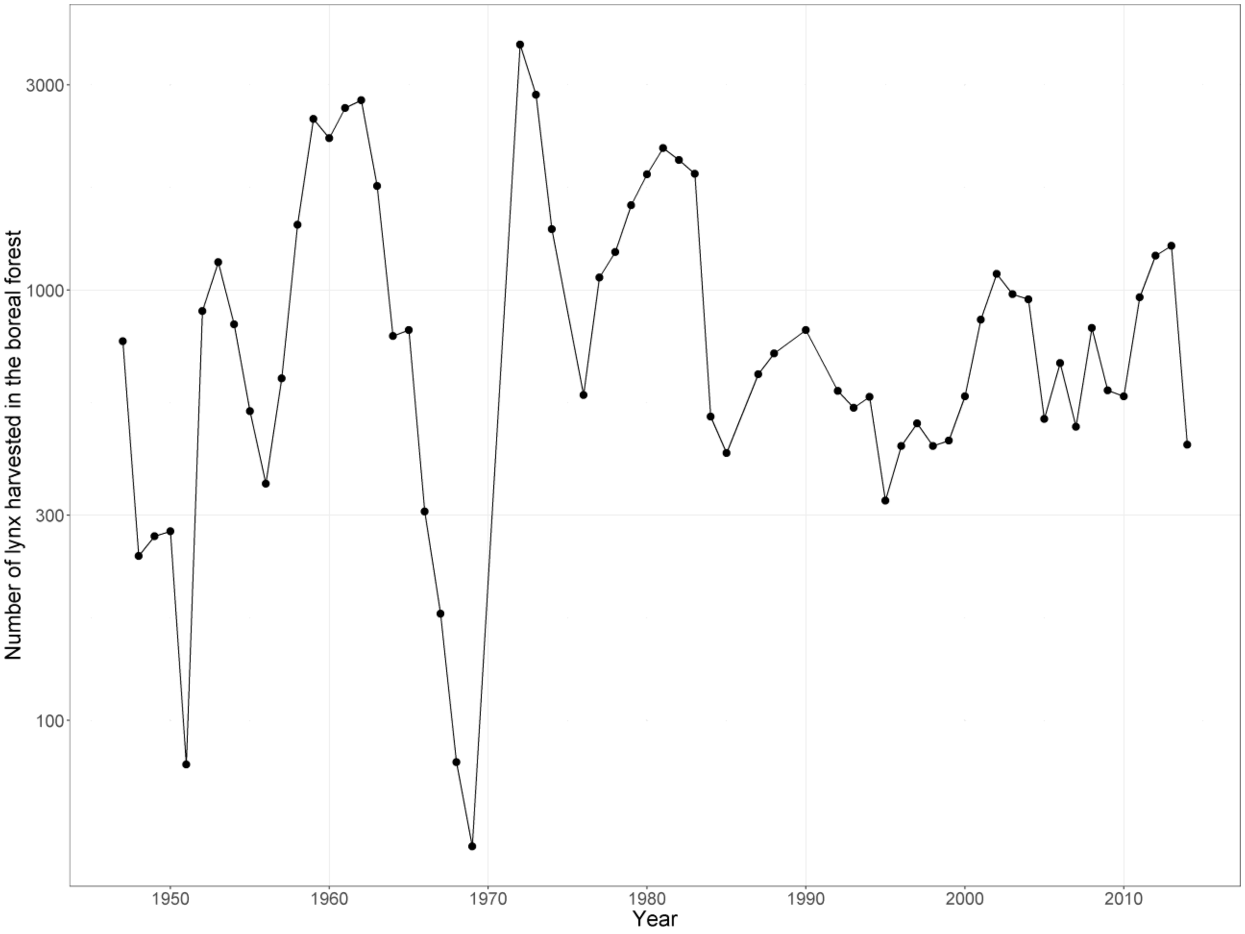

Figure S2. Number of Canada lynx harvested in the boreal forest of Ontario from 1948 to 2014. Records used to estimate the southern range at the southern boundary of the boreal forest were removed.

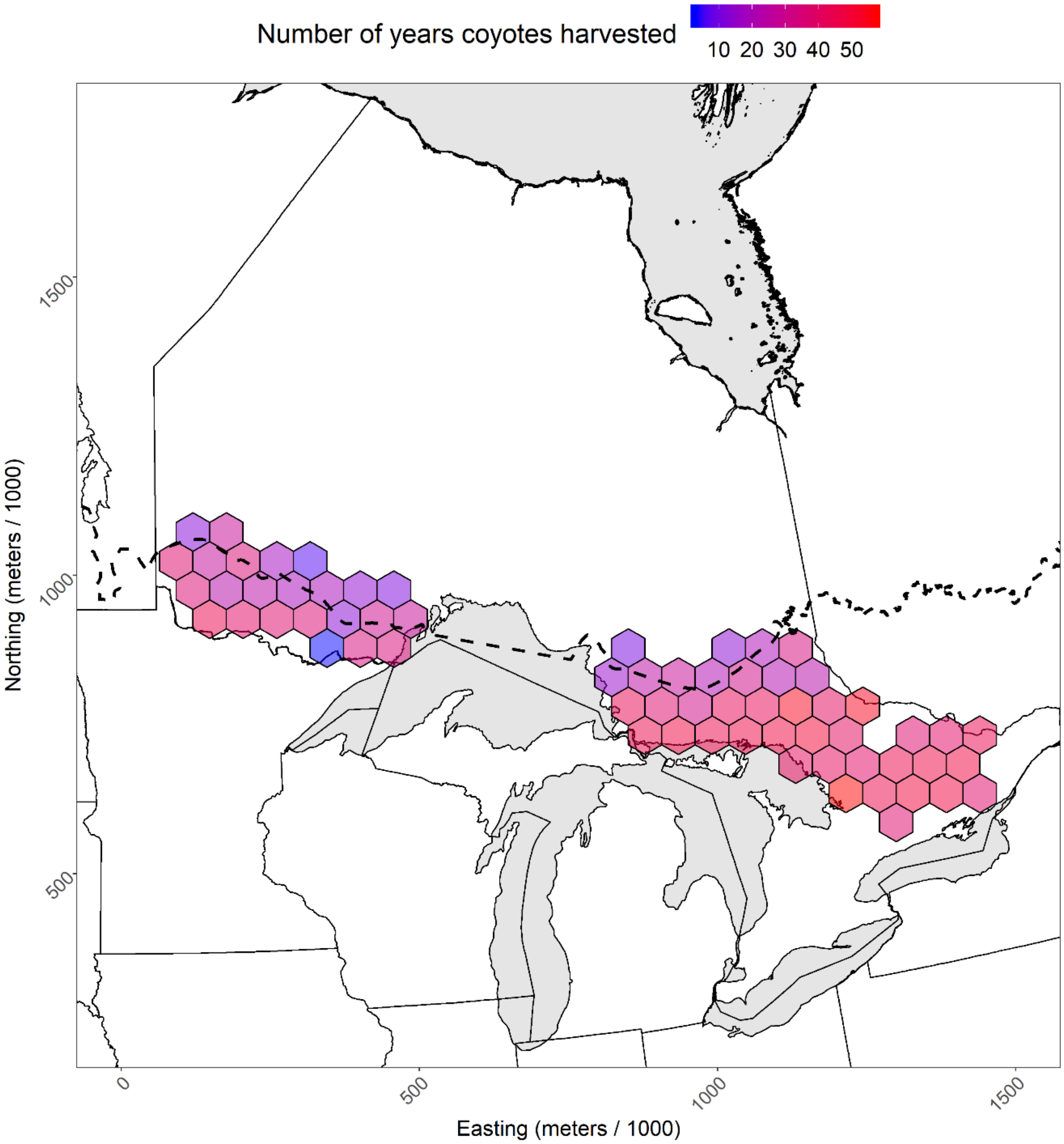

Figure S3. Number of years that coyotes were harvested within sampling units in the southern range of the Canada lynx in Ontario, Canada between 1948 and 2014. The black line is the boreal forest southern limit by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).

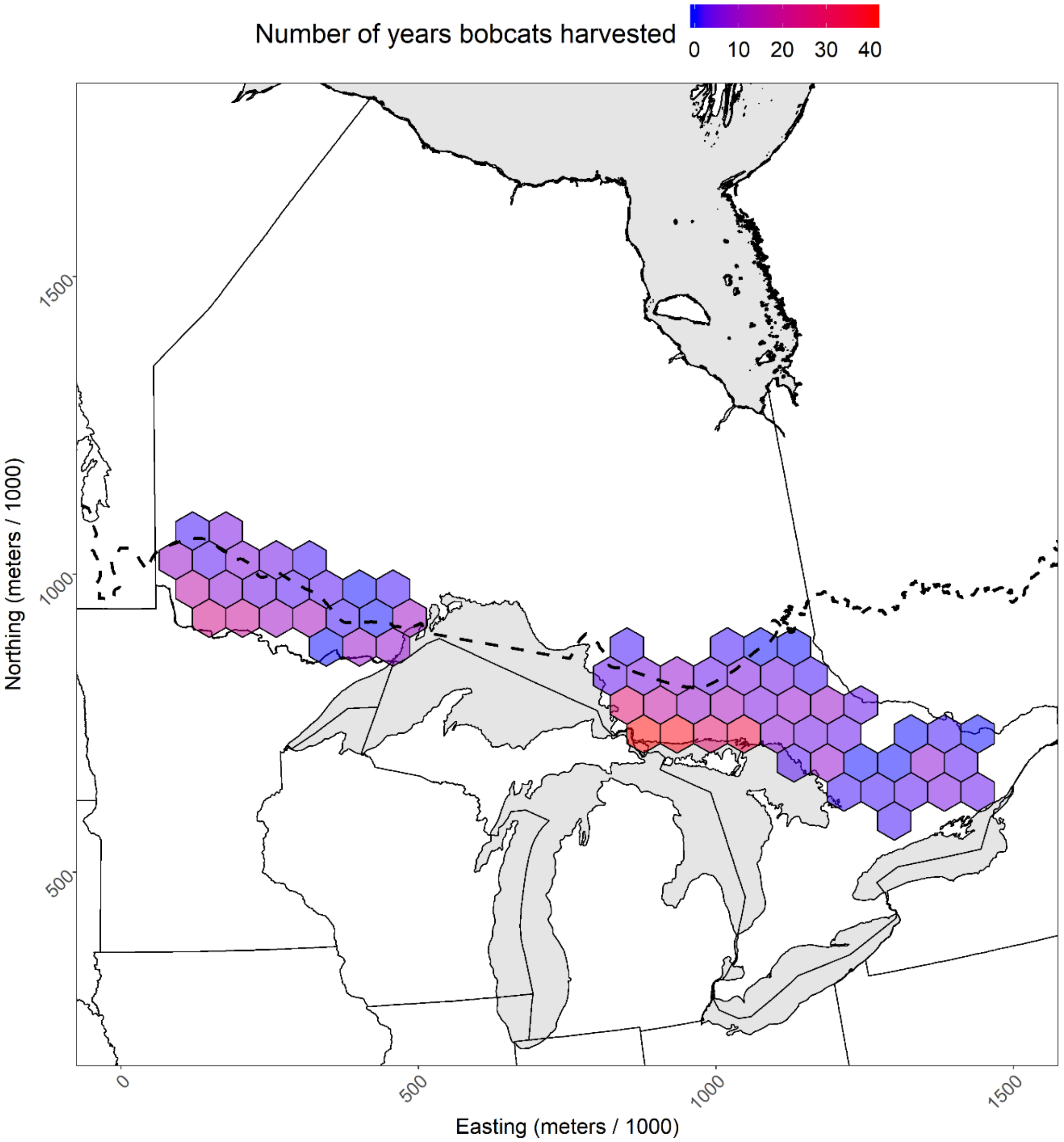

Figure S4. Number of years that bobcats were harvested within sampling units in the southern range of the Canada lynx in Ontario, Canada between 1948 and 2014. The black line is the boreal forest southern limit by Brandt (2009). Spatial layers for administrative boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/).

Chapter 4: The Relationship Between Least-Cost and Resistance Distance

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Contributions: RRM and JB conceived and designed the study; RRM ran the simulations, analyzed the data, and wrote the manuscript; JB critically reviewed the manuscript.

Abstract

Least-cost modelling and circuit theory are common analogs used in ecology and evolution to model gene flow or animal movement across landscapes. Least cost modelling estimates the least cost distance, whereas circuit theory estimates resistance distance. The bias added in choosing one method over the other has not been well documented. We designed an experiment to test whether both methods were linearly related. We also tested the sensitivity of these metrics to variation in Euclidean distance, spatial autocorrelation, the number of pixels representing the landscape, and data aggregation. We found that least cost and resistance distance were not linearly related unless a transformation was applied. Resistance distance was less sensitive to the number of pixels representing a landscape and was also less sensitive than least-cost distance to the Euclidean distance between nodes. Spatial autocorrelation did not affect either method or the relationship between methods. Resistance distance was more sensitive to aggregation in any form compared to least-cost distance. Therefore, the metric used to infer movement or gene flow and the manipulations applied to the data used to calculate these metrics may govern findings.

Introduction

Early work by Doyle and Snell [1] revealed that current in an electrical circuit travels similarly to a random walk. Two decades later McRae [2] applied this concept to model gene flow. Since then, circuit theory and associated software Circuitscape [2], has been used to simulate movement and gene flow of a multitude of species in the fields of ecology and evolution (*e.g.*, [3], [4], [5], [6], [7]). At the same time, least-cost modelling has also been commonly used for very similar applications (*e.g.*, [8], [9], [10], [11], [12]). The popularity of these methods in ecology is quickly increasing (Figure 4.1). A Google Scholar search with the query: “least-cost modelling” AND “ecology”, revealed that peer reviewed articles mentioning this approach have increased from 4 articles in 2000 to 108 in 2015. On the other hand, the search query: “Circuitscape” AND “Ecology”, revealed 0 articles in 2000 and 109 articles in 2015. Circuitscape was first conceived by McRae [2], however the name of the software was not coined in peer reviewed literature until 2007 [7], [13], [14]. Conversely, least-cost modelling in ecology has been around since the early 2000s [15], [16], [17]. While the usage of both approaches is likely to increase, few studies have investigated their quantitative differences [18], [19], [20]. Both methods have the common objective of predicting gene flow or movement between locations and taking into account the influence of the landscape. In both cases, the landscape is represented as a cost surface, where a high cost is considered highly resistant to movement. Consequently, the distance or time to travel between locations is hindered by the cost to travel through obstacles. In essence, the straight Euclidean path is deviated around obstructions causing spatial distortion that is not in accordance with Tobler’s 1st law of geography [21], [22]. Both continuous and discrete (categorical) resistance surfaces are frequently used to infer movement and gene flow of populations or individuals. Continuous resistance surfaces are frequently used to infer the effect of gradients of a continuous variable such as elevation [23], [24], snow depth [25], temperature [26], slope [27], habitat suitability [28], or species distribution [29] on the movement pattern or gene flow of a species. On the other hand, discrete resistance surfaces are often generated from land use [30] or land cover maps [31], [32].

The relationship between least cost and resistance distance has not been studied in great depth [18], [19], [20], and researchers ought to recognise the bias they might be adding when choosing one method over another. Both methods are different in the way movement is characterised. Least-cost modelling expresses movement as the least cost path between two focal points. Circuit theory expresses movement as the probability of a random walk between focal nodes [33]. The distance between nodes is then expressed as the accumulated cost of the least-cost path or the resistance distance [15], [34]. However, both distance measures are similar in accounting for the influence of the landscape on the movement or gene flow of individuals. Both measures also complement one another and have been used together for this very reason (*e.g.*, [35]). Furthermore, there is an apparent relationship between the methods. In a scenario where only one pathway exists between two nodes, the resistance distance is equal to the least-cost distance [33]. Where there are multiple independent pathways between nodes, the average least-cost distance of these pathways is equivalent to the resistance distance. Therefore, a coarse measure of the number of pathways or the redundancy between nodes is the ratio between least-cost and resistance distance [33]:

$$Redundancy = \frac{(least\text{−}cost\ distance\ )}{\hat{R}} \tag{1}$$

where R̂ is resistance distance. Least cost and resistance methods have been combined in a diverse number of different ways [35], [36], [37], [38]. However, the use of the redundancy metric is rare in the literature [18].

Recently, McClure *et al.* [20] compared the predictability of cost and resistance distance and found that least-cost distance predicted elk migration path slightly better and resistance distance predicted wolverine dispersal paths better. Also, these methods produced different results when used to find habitat patches that should be prioritized for conservation [19]. The importance of patches as connectors to facilitate dispersal was overestimated using least-cost compared to resistance distance for short or medium dispersals. Koen *et al.* [18] showed that if high quality elements of habitat were held constant at low movement cost while low quality habitat was sequentially increased, there was a positive linear change in both least-cost and resistance distance. All other responses were asymptotic for both least-cost and resistance distance. This study highlights the sensitivity of both resistance and least-cost distance to the cost weights assigned to landscape elements. Schwartz *et al.* [6] found that wolverine gene flow was more correlated to least-cost distance compared to resistance distance and both methods only converged in narrow areas. They suggested that least-cost distance may explain southern wolverine gene flow better because these populations are often found in linear habitat connected by chains of mountains. Essentially, the wolverine is restricted within this habitat and its movement behaviour and consequently its gene flow mirrors a least-cost path.

Such findings highlight the importance of investigating assumptions of both effective distance measures. Researchers should choose a movement or gene flow metric that closely matches the behavior, biology, and ecology of the focal entity. For instance, least-cost distance inherently assumes that an animal will follow the path of least resistance between focal locations [6] and resistance distance assumes multiple pathways between sites [2]. We suspect that the data used to quantify these distances are a major contributor that governs how both methods perform. In this study, we define least-cost distance as the cost-distance of the least-cost path between focal points [34]. This metric is often named the accumulated cost and is occasionally confused with the least-cost path length. It is important to recognize the difference, because this latter metric is highly correlated with Euclidean distance and consequently is a poor measure of connectivity [34], unless there is high uncertainty about cost weights [18].

We sought to better understand the difference between these commonly used methods to estimate effective distance between locations by comparing their outcomes on landscapes simulated using spatially correlated random fields. Our prior understanding was that these methods were related by a quantity referred to as redundancy (Equation 1). In addition, we also thought that the number of pathways between focal points monotonically decreases with the Euclidean distance and spatial heterogeneity. Our reasoning was that Euclidean distance and heterogeneity limit movement by reducing the number of pathways between focal areas. Thus, increasing the distance between focal points and the degree of spatial autocorrelation should lead to a divergence between least-cost and resistance distance. We also thought that the relationship between methods could be influenced by the number of pixels representing the landscape. Our logic was that the number of pathways between nodes increases monotonically with the number of pixels. Therefore, as the number of pixels increases, we should also see an equivalent increase in redundancy. Finally, we also expected that aggregation in the form of spatial and thematic accuracy should lead to convergence of the two methods. Our reasoning was that aggregation in any form should lead to a reduction in the number of pathways between focal points and subsequently both methods converge with increasing aggregation. Aggregation is very commonly used, since the algorithms using least-cost distance are processor and memory intensive, leading many researchers to spatially aggregate their data at coarse resolutions [6], [39], [40].

Materials and Methods

Landscape creation

We used unconditional Gaussian simulations [41], [43], also known as spatially correlated random fields [44], in the ‘gstat’ package [45] of the R statistical language [46] to generate landscape simulations.

To determine linearity, the effect of Euclidean distance, spatial autocorrelation, and the response of these methods to aggregation we simulated 1,000 landscapes with varying degrees of spatial autocorrelation. We first generated template landscapes with spatial dimensions of 1,000 x 1,000 units; equivalent to 1 million pixels. Next, for each of these landscapes, we created an exponential variogram model with a sill of 0.025 and we assigned a random spatial range. The range of each of these models was randomly sampled from a bounded uniform distribution between 1 and 1000 units. As the range increased from 1 to 1000, so did the degree of spatial autocorrelation between neighbouring pixels. We then predicted the model into Cartesian space as a continuous raster surface, scaled between 1 and 1000 integer values. These values represented landscape resistance or cost of movement, where a high value of 1000 had greater cost of movement. Subsequently, with these same landscapes, we independently performed spatial and thematic aggregation to determine their effect on the congruence between least-cost and resistance distance. We aggregated each landscape by a factor of 1 to 20 to simulate different levels of spatial aggregation. In parallel, we aggregated the cost values into a random number of discrete groups using quantiles to generate different levels of thematic resolution. The number of categories ranged from 2 categories (*i.e.*, a patch-matrix landscape) to 20 possible values (*e.g.*, a land use or land cover classification). Essentially, we used the cost values to generate a ramp of discrete classifications and compared these to the continuous cost landscape.

To determine the effect of the number of pixels on the relationship between least-cost and resistance distance, we simulated an additional 1,000 landscapes with varying number of pixels and degree of spatial autocorrelation. We first assigned a square spatial dimension to each perspective landscape ranging from 100 to 1000 units. This generated square blank landscapes that had from 10,000 to 1 million pixels. As in the previous analysis we modelled this spatial extent with a variogram with a sill of 0.025 and a spatial range randomly sampled for a uniform distribution. We restricted the creation of landscapes that had duplicate representations, that had less than 10,000 pixels, or that had a spatial autocorrelation range larger than the dimension of the spatial extent (*e.g.*, 1000 units).

In both sets of simulations, for each resistance surface generated, we randomly placed 15 focal nodes on the landscape and calculated pairwise measures of least-cost and resistance distance between all node pairs. To reduce edge effect, we did not place sites within a buffer zone within 10% of a landscape's dimension [47]. To calculate resistance distance, we used Circuitscape [2]. To calculate the least-cost distance we used Dijkstra's algorithm weighted by cost that is implemented in the cost distance function in the 'gdistance' R package [48], [49]. We configured analyses in all platforms to use pairwise modelling with 8 neighbours. We used the average resistance to calculate these effective distances. We also tested average conductance but found no noticeable differences in our subsequent results.

Opportunistically, we also compared resistance distance to an alternative method that directly estimates the commute-time or the expected time it takes for a random walk from one node to another. Given that commute-time is easily calculated in R, we were interested to evaluate whether commute-time and resistance distance were equivalent, as both reflect the underlying properties of a random walk. To calculate the commute-time, we used the algorithm given by Fouss *et al.* [50] implemented in the commute-time distance function in the 'gdistance' R package [48]. We expected a direct, proportional relationship between these distance measures [33], [51].

Statistical analysis

We compared the effective distance between all pairs for both methods for each landscape represented by 1 million pixels. To determine whether linearity existed between least-cost and resistance distance, and to test the effect of Euclidean distance and spatial autocorrelation on the relationship between least-cost and resistance distance we compared the pairwise distances calculated by each method on each landscape of 1 million pixels with a measure of rank correlation. We did not want to bias our analysis by assuming linearity between both metrics, consequently we used a Spearman’s rank correlation (p). In addition, our prior analyses indicated that these measures were not linearly associated (See results). To determine the effect of the number of pixels representing a landscape on the relationship between these methods we calculated the rate of change of the distances of both measures against the associated number of pixels representing the landscape. We additionally verified the relationship between methods by comparing their distances with a Spearman’s rank correlation on all landscapes represented by 1 million pixels. Finally, to determine the effect of aggregation, we first assessed the concordance of least-cost and resistance distance before aggregation and we then compared this baseline value to those after aggregation. Our measure of change due to aggregation was the difference in the rank correlation (Δp) between the baseline landscape of 1 million pixels and the aggregated landscape for both types of aggregation. We assessed the variability of each method due to aggregation by comparing their measures before and after aggregation with a Spearman’s rank correlation.

Results

Linearity between methods

The relationship between least-cost distance and resistance distance was non-linear (Figure 4.2). The response was curvilinear and exponential. When we square-root transformed the least-cost distance or squared the resistance distance the response was linearized (Figure S1 and S2). The distribution of the rank correlation between least-cost and resistance distance for all 1,000 landscapes ranged from 0.25 and 0.93 ($\mu = 0.720$ and $\sigma = 0.101$; S3 Fig). The relationship between resistance distance from Circuitscape and commute-time was linear ($p = 0.87$ for a subset of 5,000 paths; Figure S4). The distribution of the rank correlation between resistance distance and commute-time for all 1,000 landscapes did not vary much from the average ($\mu = 0.998$ and $\sigma = 0.001$).

Euclidean distance and spatial autocorrelation

Both least-cost and resistance distance increased monotonically with Euclidean distance (Figure 4.3). Least-cost distance increased at a much higher rate compared to resistance distance (slope = 345 vs. 0.28). Euclidean distance explained 71.0% of the variation in least-cost distance and only 18.9% of variation in resistance distance. In general, a 100 unit increase in Euclidean space between two focal points led to only a 28 unit increase in resistance distance, compared to a 34,500 unit increase in least-cost distance. The degree of spatial autocorrelation of a landscape did not seem to affect the estimates of either method (Figure S5) and did not affect their relationship (Figure S6).

Number of pixels

For both least-cost and resistance distance there was an exponential response with the number of pixels representing the landscape (Figure 4.4). In addition, this trend was stronger for least-cost compared to resistance distance. A 100% increase in the number of pixels led to a 50% increase in least-cost distance and only a 7% increase in resistance distance. The trend for least-cost distance was predominantly explained by the number of pixels ($r^2 = 0.53$) but this was not the case for resistance distance ($r^2 = 0.09$). The Spearman's rank correlation calculated between both methods between all pairwise combinations of the 15 nodes decreased as the number of pixels representing the landscape increased (Figure 4.5). This indicated that the agreement between these effective distances decreased as the number of pixels (or the number of pathways) through the landscape increased. For instance, the rank correlation between methods for a landscape represented by 100,000 pixels would be ~0.78, for a landscape represented by 1 million pixels would be approximately 0.73, and a landscape represented by 10 million pixels would be ~0.67. Therefore, we should not expect the same degree of agreement between methods on landscapes represented by different numbers of pixels. In other words, the magnitude of agreement between measures depends on the number of pixels representing the landscape.

Aggregation

Both spatial and thematic aggregation decreased the rank correlation between least-cost and resistance distance (Figure 4.6). However, spatial aggregation had a greater impact on the rank correlation between the two methods. In addition, we tested whether the methods themselves varied independently due to both types of aggregation. We found that spatial aggregation did not affect least-cost distance but did affect resistance distance (Figure 4.7). We also found that thematic aggregation affected both methods, but resistance distance to a lesser degree than least-cost distance (Figure 4.8). Generally, resistance distance was more sensitive to both types of aggregation.

Discussion

We found that least-cost and resistance distance did not have a direct linear response, but rather, were curvilinear. This was not surprising, as redundancy should scale with area, which is a square. We could linearize the relationship between these measures by using a square-root transformation of least-cost distance or a squared transformation of resistance distance (Figure S1 and S2):

$$redundancy' \sim \frac{\sqrt{least-cost\ distance}}{\hat{R}} \sim \frac{least-cost\ distance}{\hat{R}^{2}} \qquad (2)$$

where redundancy’ is the linearized version of redundancy after transforming least-cost or resistance distance. In any case, these methods produce somewhat the same rank order (Figure S3), but there are many cases where their association is quite low (where $p < 0.7$). We can interpret Figure S3 as a probability distribution and infer that in 50% of landscapes the rank correlation between least-cost and resistance distance is < 0.72. This means, 50% of the time the methods have poor agreement in the rankings of their distances. Depending on the type of analysis these differences could be quite important (*e.g.*, [6,19]). Researchers should not use one method as an alternative to the other, since they are not linearly related (Figure 4.2) and do not agree 50% of the time. They represent difference concepts and additionally function on different spatial and thematic scales.

We also found that commute-time is very similar to resistance distance (Figure S4), which may be of interest for researchers that use the R statistical language. The commute-time function in the ‘gdistance’ package in R can be used as an alternative to estimate resistance distance in Circuitscape.

Both least-cost and resistance distances estimates responded much differently to the Euclidean distance between focal points, when measured on a log-log scale. They both have linear relationship with Euclidean distance, but the rate of increase of least-cost distance was ~500 times higher than resistance distance. Hence, least-cost distance is more sensitive to changes in Euclidean space when compared to resistance distance. Seeing as Euclidean distance alone explains ~71% of the variance in least-cost distance we could easily approximate least-cost distances on a landscape by simply knowing a few pairwise measures; we could estimate least-cost distance from the Euclidean distance without using Dijkstra’s shortest path algorithm [49].

We had previously thought that spatial autocorrelation would play an important role in explaining the relationship between these methods. However, we did not find any evidence to support this idea (Figure S5 and S6). This suggests that spatial autocorrelation is not an important consideration when choosing a method for estimating effective distance.

Both metrics also responded differently to the number of pixels representing a landscape (Figure 4.4). This relationship is quite similar to the Euclidean distance (Figure 4.3), but in this case the trends are on a log-log scale. Once again, resistance distance had a much smaller rate of change with the number of pixels compared to least-cost distance. Most of the variance in least-cost distance was explained by the number of pixels representing the landscape. If we added the log-transformed Euclidean distance as an explanatory variable, the amount of total variance explained increased to 87.4% for least-cost distance and only 30.6% for resistance distance. This shows that least-cost distance is sensitive to the Euclidean distance and the number of pixels representing a landscape. This is not true to the same extent for resistance distance. Also, we found that there is a gradual trend between the number of pixels representing a landscape and the agreement between the rank orders of both methods (Figure 4.5). We suggest that there is a baseline correlation between these methods that is a function of the number of pixels. In other words, on landscapes represented by more than 10 million pixels we would expect higher rank correlation compared to a landscape represented by 1 million pixels. This suggests that it should be rare to have a high rank correlation between these methods using data represented by relatively few pixels. It is therefore not surprising that Avon and Bergès [19] found different results when comparing the two methods. Their landscapes were of 7,090 km^2 and 31,700 km^2 and their spatial data resolution was 100 m. The number of pixels representing these landscapes was about 0.79 and 3.17 million pixels. Therefore, the baseline Spearman's rank correlation between these methods would have been between 0.70 and 0.73.

Finally, aggregation is quite common for these types of analyses (*e.g.*, [6,39]). Data manipulation eventually affects the relationship between the methods (Figure 4.6). Spatial aggregation affects the relationship the most and is a common approach used to reduce processing time and virtual memory usage. For landscapes that are represented by 1 million pixels, spatial aggregation can change the relationship between least-cost and resistance distance on average by 0.11 *p* units, no matter the degree of spatial aggregation. In many cases, data of much finer resolution are represented by many more pixels, consequently aggregation will affect these methods more. It was previously common knowledge that spatial aggregation did not affect resistance distance much, but our results suggest that resistance distance is more sensitive than least-cost distance (Figure 4.7-8). In fact, McRae *et al.* [33] noted that the pairwise resistance distance between focal nodes from a finer scale habitat map at a resolution of 1000 x 1000 pixels compared to its coarser version of 100 x 100 were highly correlated ($R^2 = 0.963$; [33]). However, we found that spatial aggregation by a factor ranging between 2 to 20 produced on average an R^2 of 0.935 (We squared Spearman's rank correlation). However, we did not test spatial aggregation of a factor of 100, such as McRae *et al.* [33]. We did find that a 20-fold aggregation produced a correlation (R^2) between resistance distance of 0.89 (Figure 4.7). We do suspect an asymptotic response of this correlation.

Conclusions

In summary, least-cost and resistance distance are not linearly related unless a transformation is applied to either metric. The least-cost distance is partly a function of the number of pixels representing the landscape and the Euclidean distance between focal points. Resistance distance is less sensitive to these factors. Spatial autocorrelation does not affect either method or their relationship. The agreement between these methods is affected by the number of pixels representing the landscape and aggregation. The former is explained by the fact that resistance distance is more sensitive to aggregation than least-cost distance. Consequently, data and data manipulations may govern the differences between these methods and their independent outcome, but not the actual landscape entity being studied. Our findings are relevant for users who wish to evaluate landscape connectivity in a variety of contexts [14], [15], [52]. Researchers should investigate how closely both methods match the biology, behaviour, and ecology of their focal entity. Whether studying gene flow or movement, the biological meaning of least-cost or resistance distance should be appropriate.

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Figures

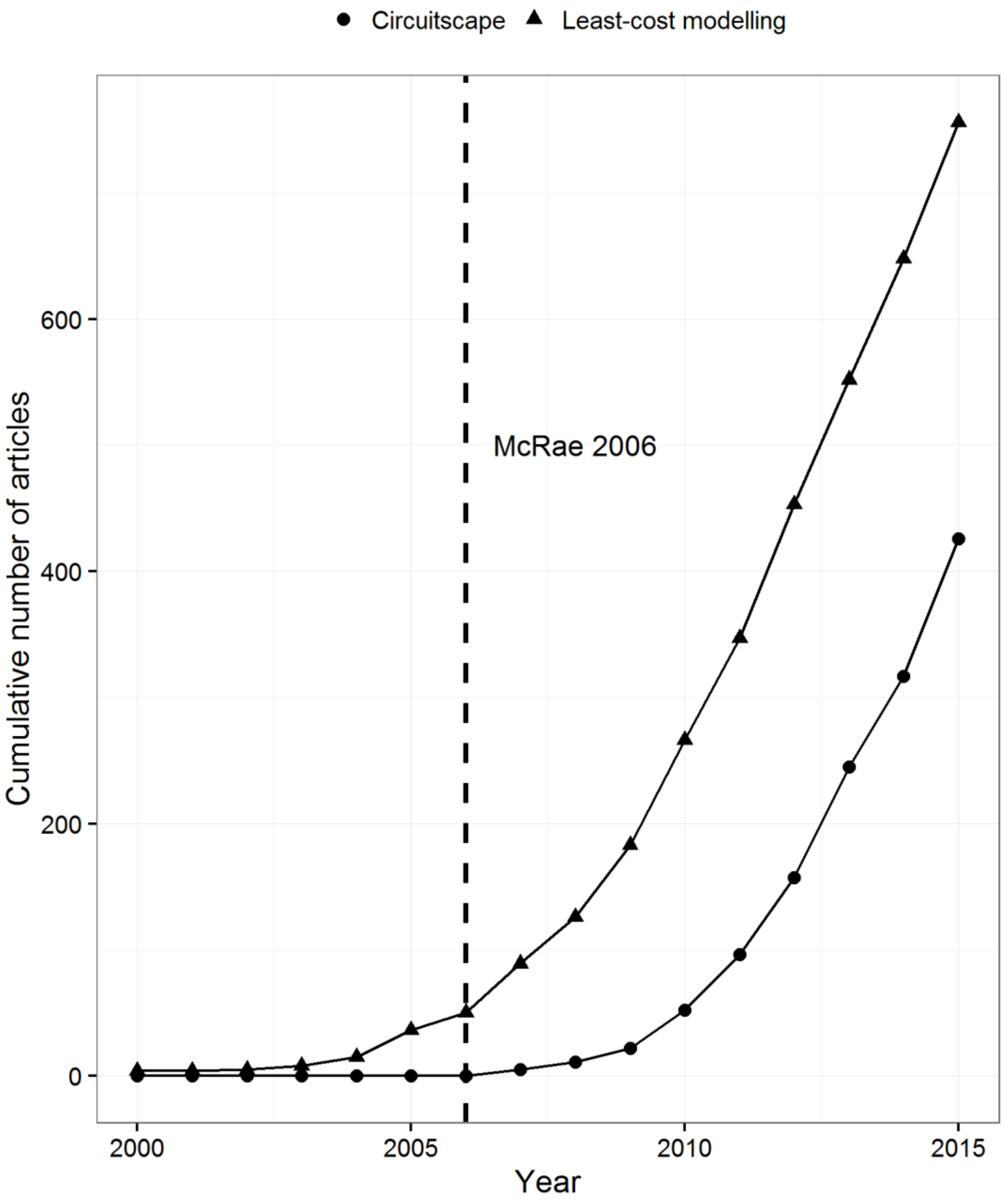

Figure 4.1. The use of least-cost modelling and circuit theory in ecology. Cumulative increase in the number of Google Scholar articles that have mentioned Circuitscape and least-cost modelling in the field of Ecology since 2000.

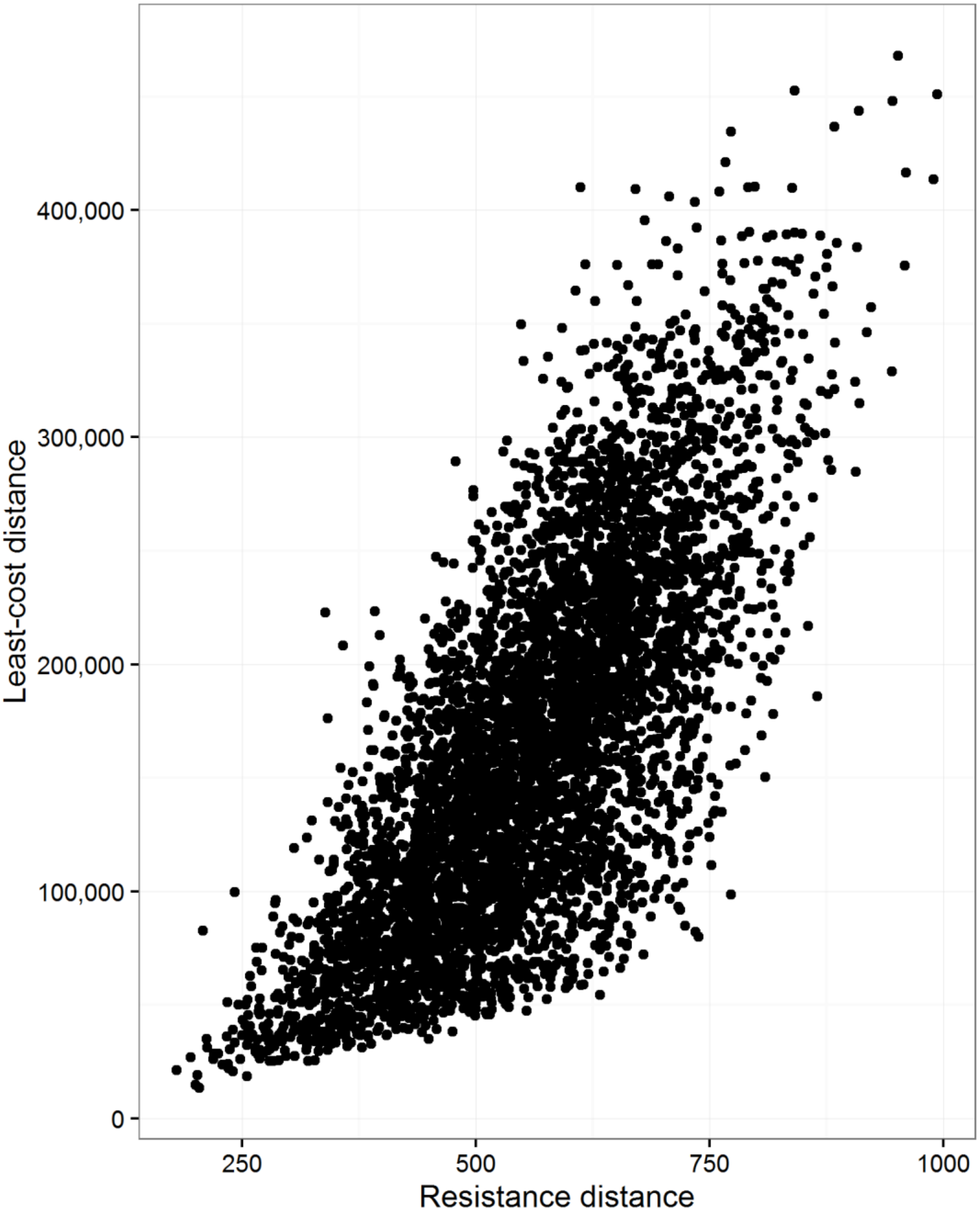

Figure 4.2. The relationship between least-cost and resistance distance for a subset of 5,000 random pairs sampled from 1000 different simulated landscapes (p = 0.731). We had to randomly subset the data to make the figures more visually appealing, since there were 105,000 actual points. Landscape size (number of pixels) was held constant at 1,000,000.

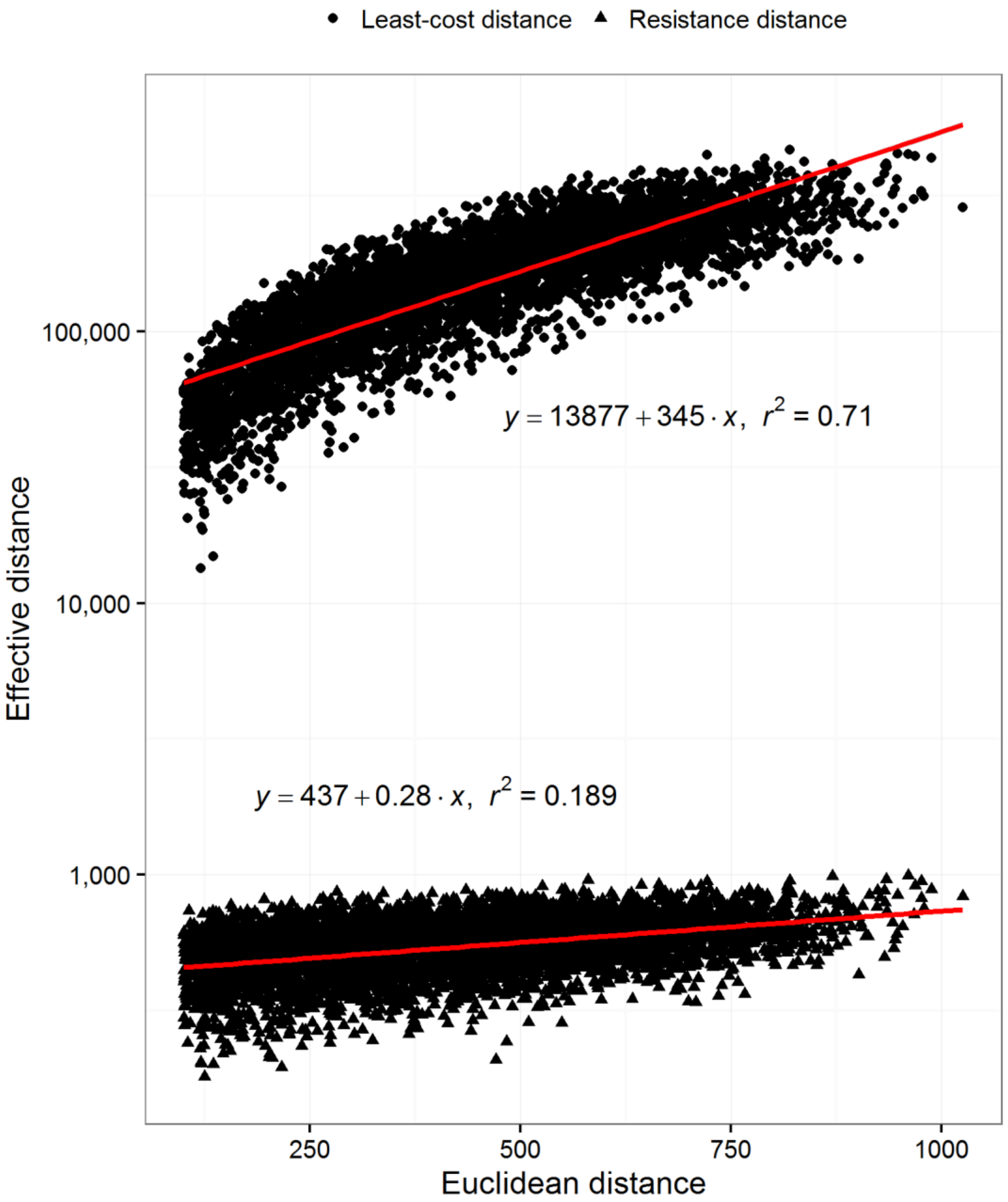

Figure 4.3. The effect of Euclidean distance on both methods for a subset of 5,000 random paths sampled from 1000 different simulated landscapes represented with 1 million pixels or nodes. The y-axis in this graph is on a logarithmic scale for visualization purposes only. Least-cost distance increases linearly with Euclidean distance while resistance distance increased linearly to quite a lesser extent. Landscape size (number of pixels) was held constant at 1,000,000.

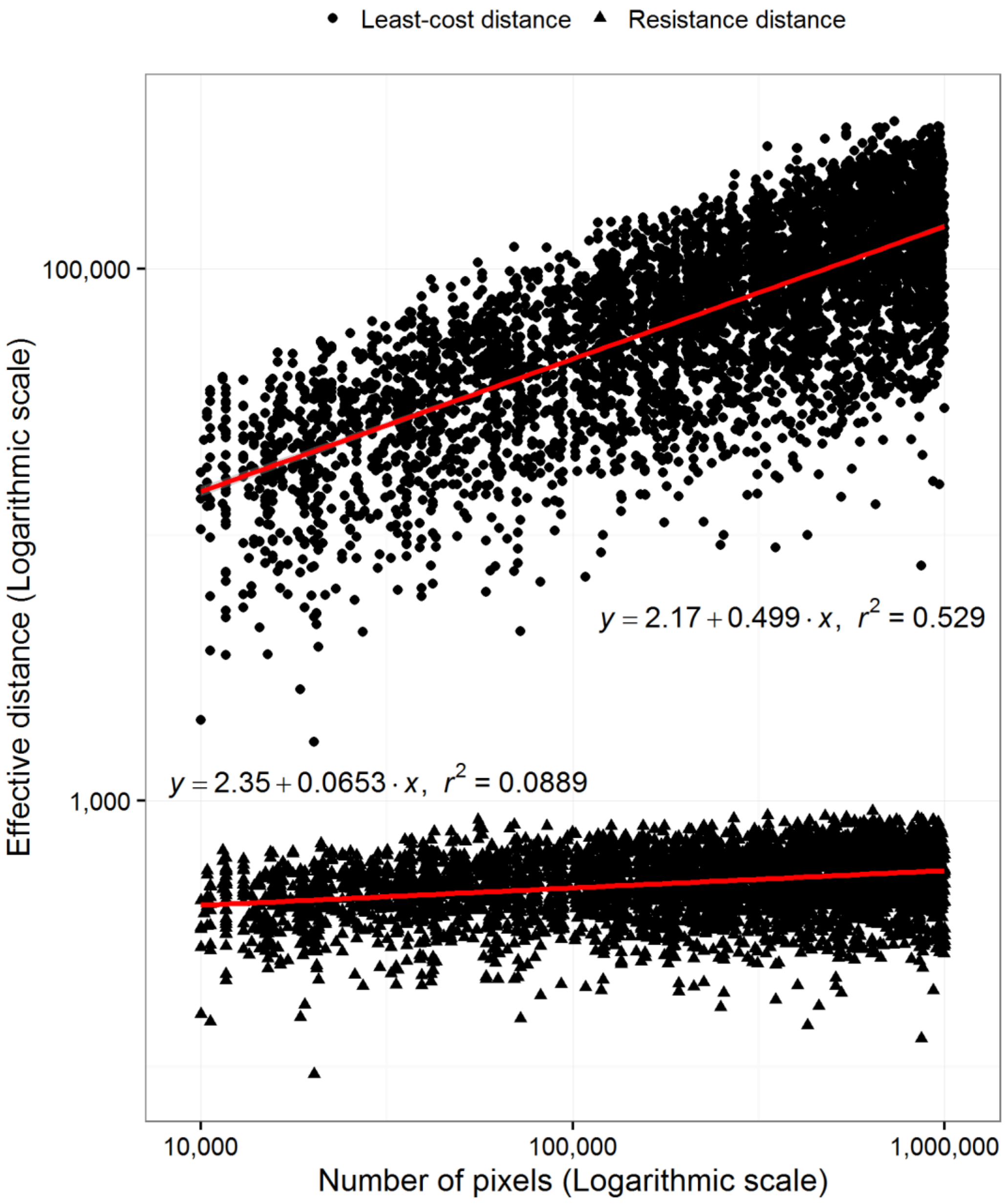

Figure 4.4. The effect of the number of pixels representing a landscape. The least-cost and resistance distance in relation with the varying number of pixels for a subset of 5,000 random paths sampled from 1,000 different landscapes with varying degrees of spatial autocorrelation and number of pixels representing the landscape. Both axes are on a logarithmic scale. In this case both the response and explanatory variables were log-transformed to calculate the linear model. Landscape size (number of pixels) is varied from 10 thousand to 1 million pixels.

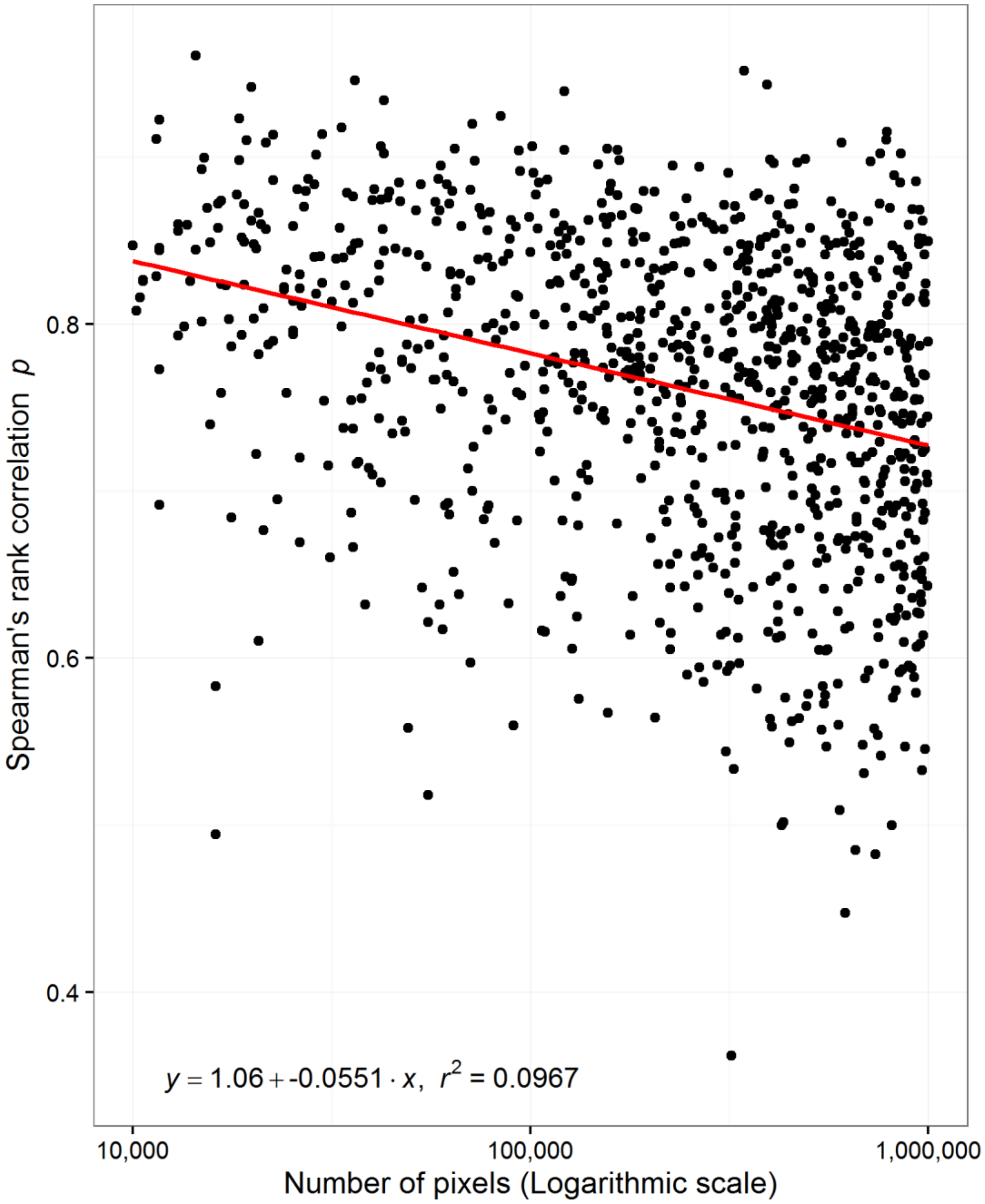

Figure 4.5. The number of pixels and rank order agreement. The rank agreement (p) between least-cost distance in relation with the log transformed number of pixels representing 1,000 different landscapes with varying spatial autocorrelation. The x-axis is on a logarithmic scale. Landscape size (number of pixels) is varied from 10 thousand to 1 million pixels.

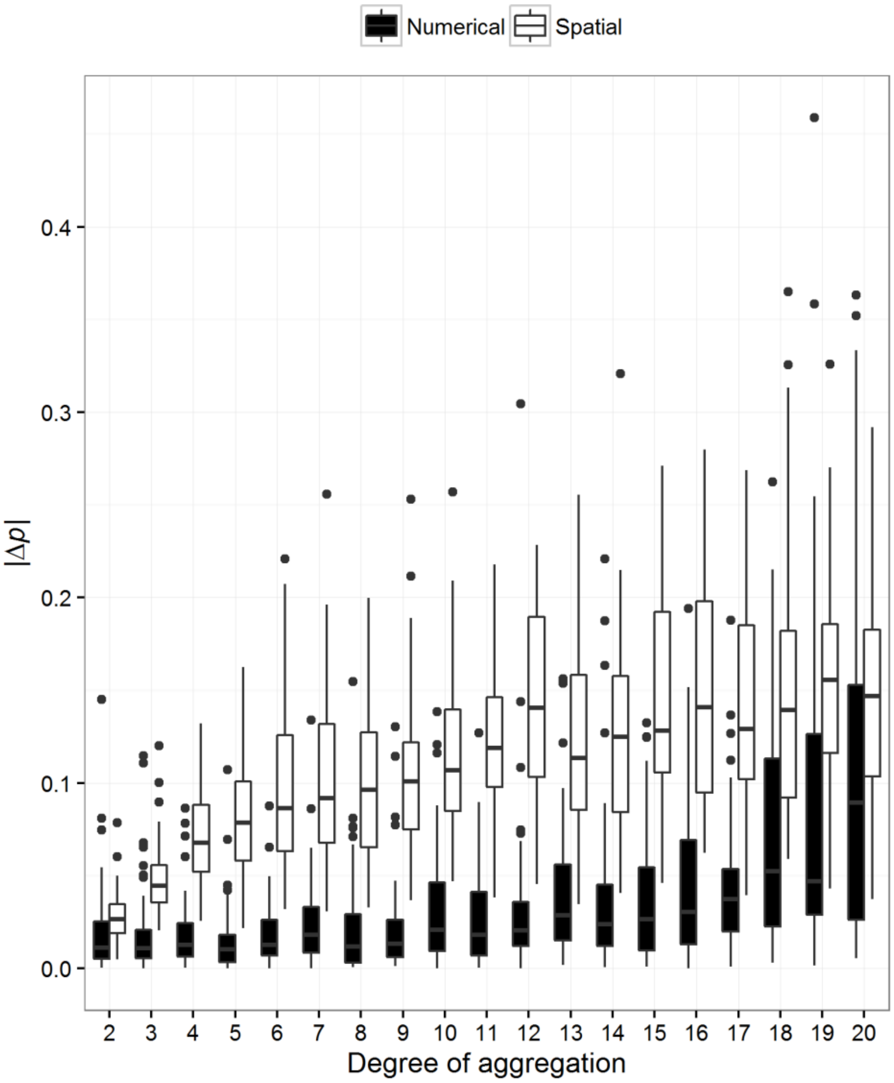

Figure 4.6. The effect of aggregation on the relationship between least-cost and resistance distance. One thousand landscapes were simulated with varying degrees of spatial autocorrelation and least-cost and resistance distance were calculated between 15 sites. The Spearman's rank correlation (p) between these methods was then calculated. These landscapes were then, in parallel, spatially and thematically aggregated by a random factor between 2 and 20. Pairwise distances were once again calculated and subsequently the rank correlations. We then deducted these subsequent rank correlations from the baseline correlations. Thus, |Δp| is the absolute change in rank correlation between methods after aggregation. The degree of spatial aggregation is simply the spatial aggregation factor. The degree of thematic aggregation is '22 - the number of discrete classes'. This means that if cost values were aggregated into 2 discrete classes the degree of thematic aggregation was 20. This figure illustrates that both spatial and thematic aggregation increase the difference between the rankings of the distances of both methods. Consequently, these methods increasingly disagree as aggregation increases.

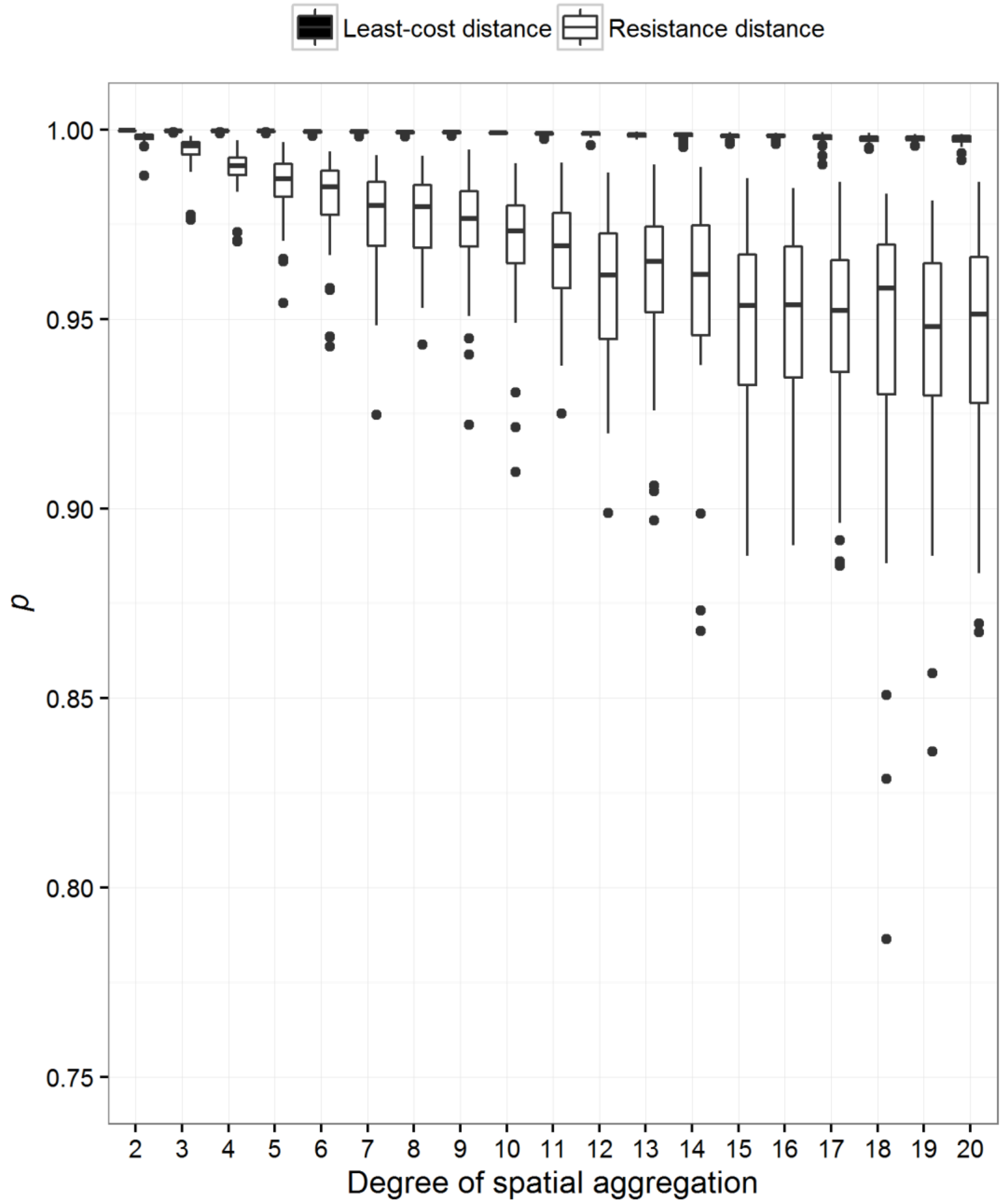

Figure 4.7. The effect of spatial aggregation on least-cost and resistance distance. One thousand landscapes were simulated with varying degrees of spatial autocorrelation. Least-cost and resistance distance between 15 sites was then calculated for all landscapes. These landscapes were then spatially aggregated by a random factor between 2 and 20. Pairwise distances were once again calculated. We then calculated the Spearman's rank correlation between each method before and after aggregation. The degree of spatial aggregation is simply the spatial aggregation factor. This figure illustrates the effect of spatial aggregation on either method. Least-cost distance is not affected by spatial aggregation, but the effect of aggregation on resistance distance monotonically increases with the degree of spatial aggregation.

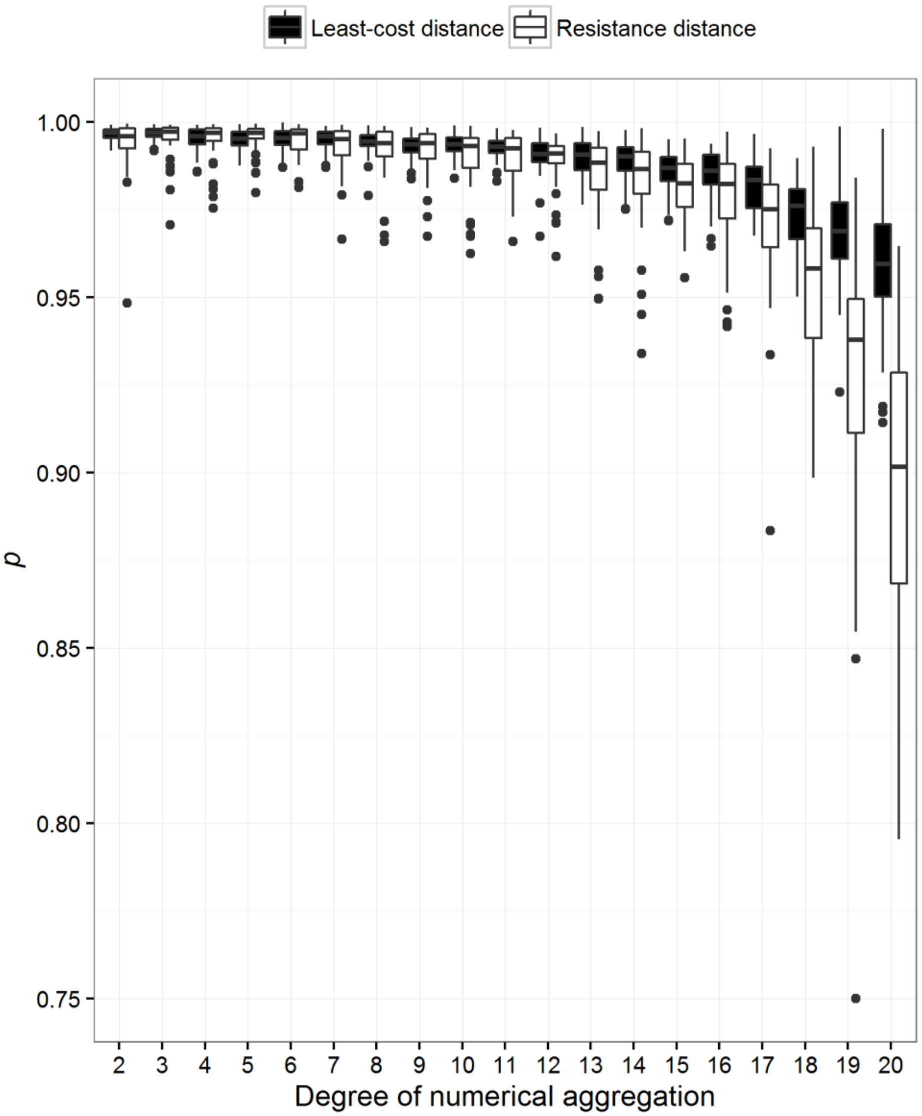

Figure 4.8. The effect of thematic aggregation on the relationship between least-cost and resistance distance. One thousand landscapes were simulated with varying degrees of spatial autocorrelation. Least-cost and resistance distance between 15 sites was then calculated for all landscapes. The cost values on these landscapes were then aggregated within discrete categories. The number of categories ranged from 2 to 20 discrete cost values. A cost surface with 20 discrete cost values would represent a land use land cover map and 2 discrete cost values would represent a binary surface. The degree of data aggregation is '22 - the number of discrete classes. This means that if cost values were aggregated into 2 discrete classes the degree of thematic aggregation was 20. Pairwise distances were once again calculated. We then calculated the Spearman's rank correlation between each method before and after aggregation. This figure illustrates that thematic aggregation decreases the agreement between the rankings of the distances. The effect is more apparent for resistance distance compared to least-cost distance.

Supplemental Figures

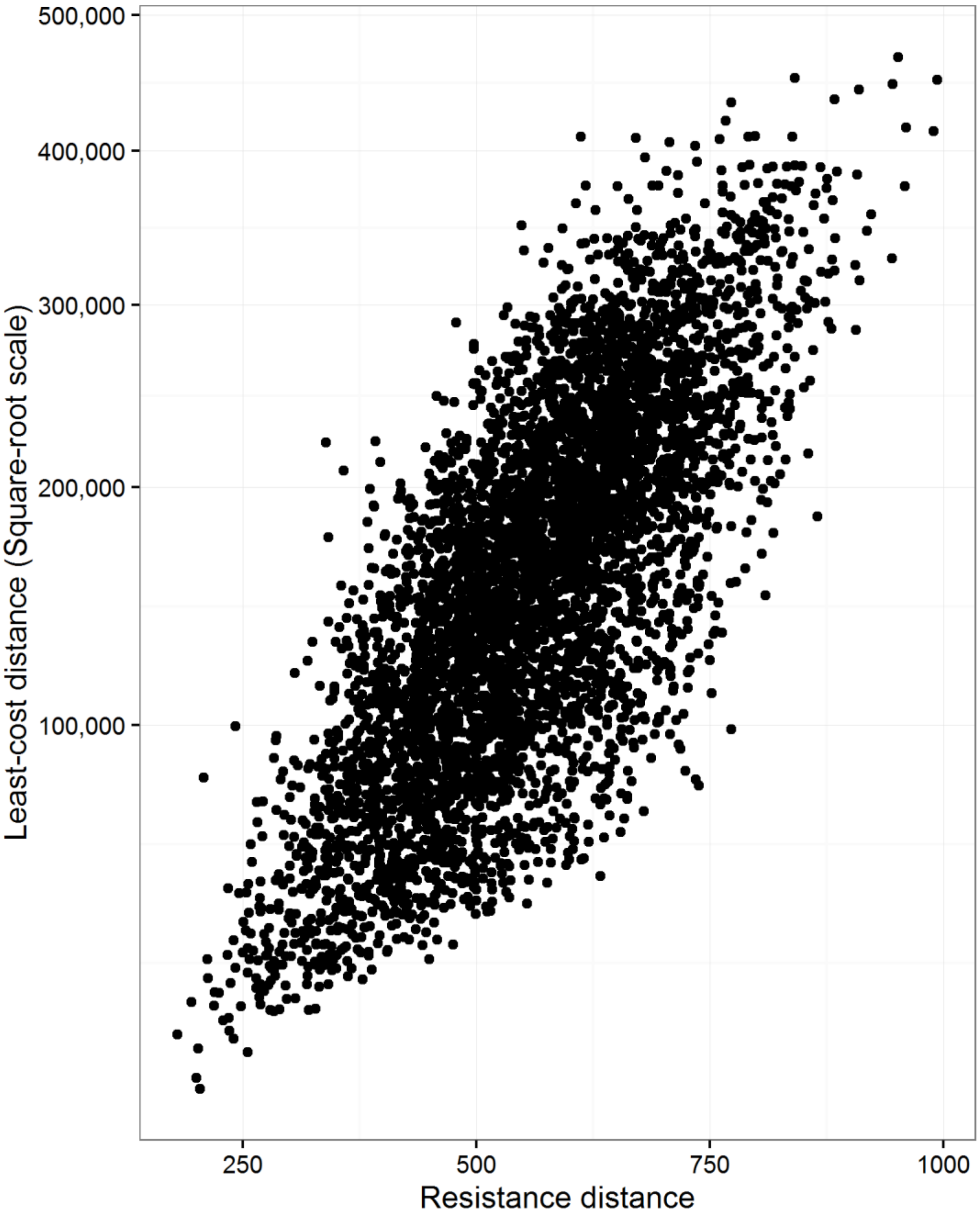

Figure S1. The relationship between square-root of least-cost and resistance distance for a subset of 5,000 random pairs sampled from 1000 different simulated landscapes. We had to randomly subset the data to make the figures more visually appealing, since there are 105,000 actual points. Landscape size (number of pixels) is held constant at 1,000,000.

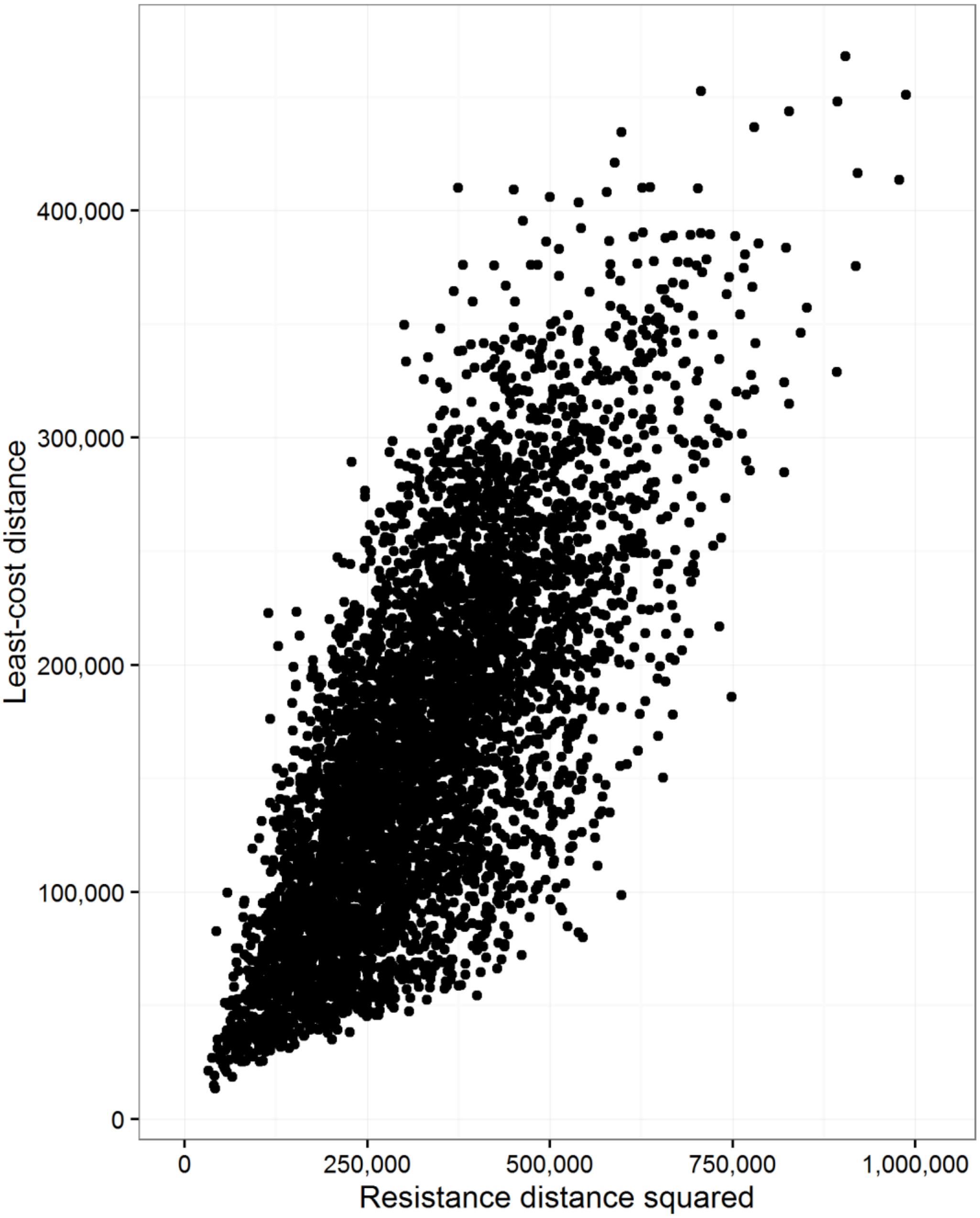

Figure S2. The relationship between least-cost and resistance distance squared for a subset of 5,000 random pairs sampled from 1000 different simulated landscapes. We had to randomly subset the data to make the figures more visually appealing, since there are 105,000 actual points. Landscape size (number of pixels) is held constant at 1,000,000.

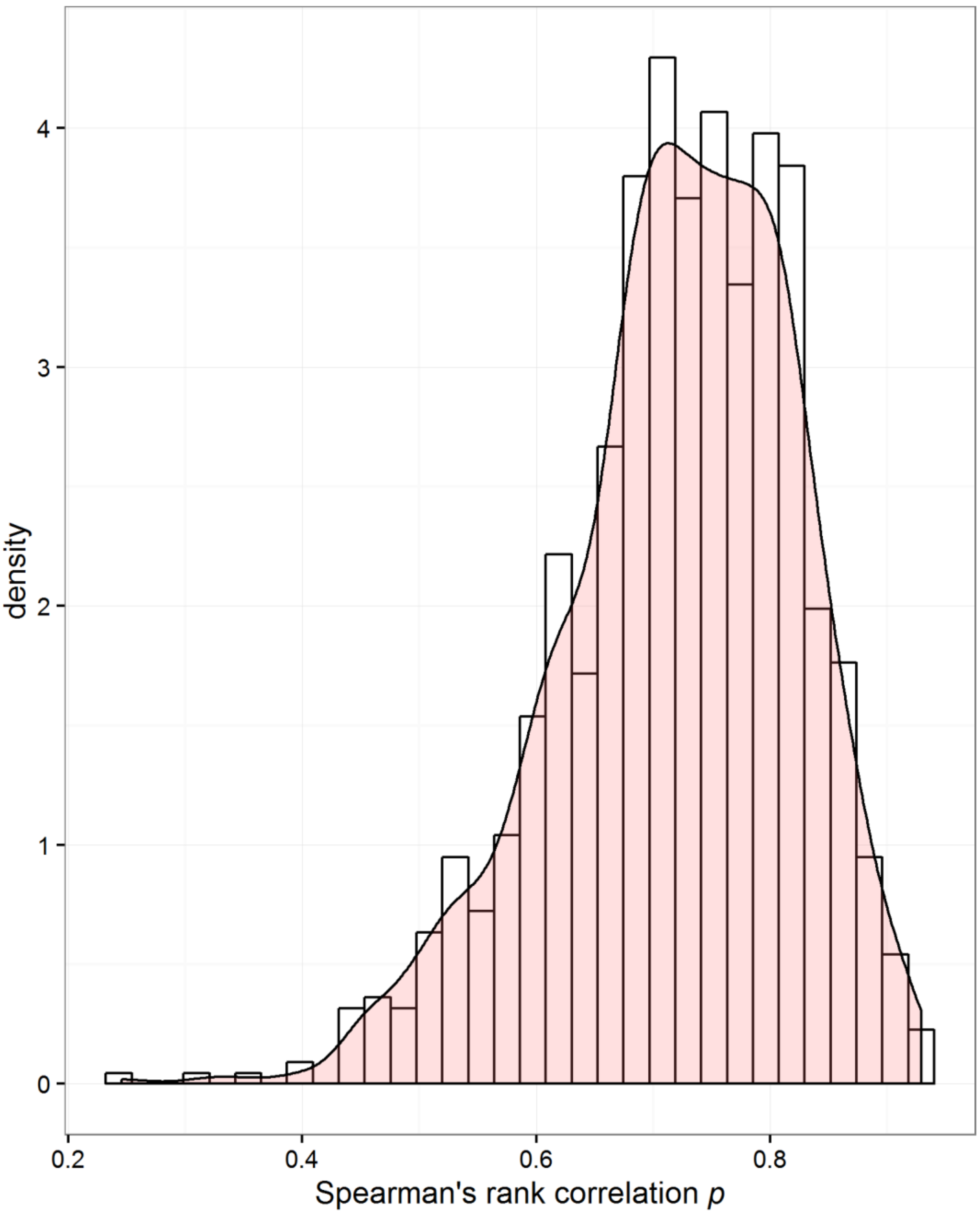

Figure S3. The agreement between the rank order of both methods. The distribution of the Spearman's rank correlation between least-cost and resistance distance for 15 randomly placed pairwise focal points on 1000 generated landscapes (μ = 0.720, σ = 0.101, range: 0.246-0.929). Landscape size (number of pixels) is held constant at 1,000,000.

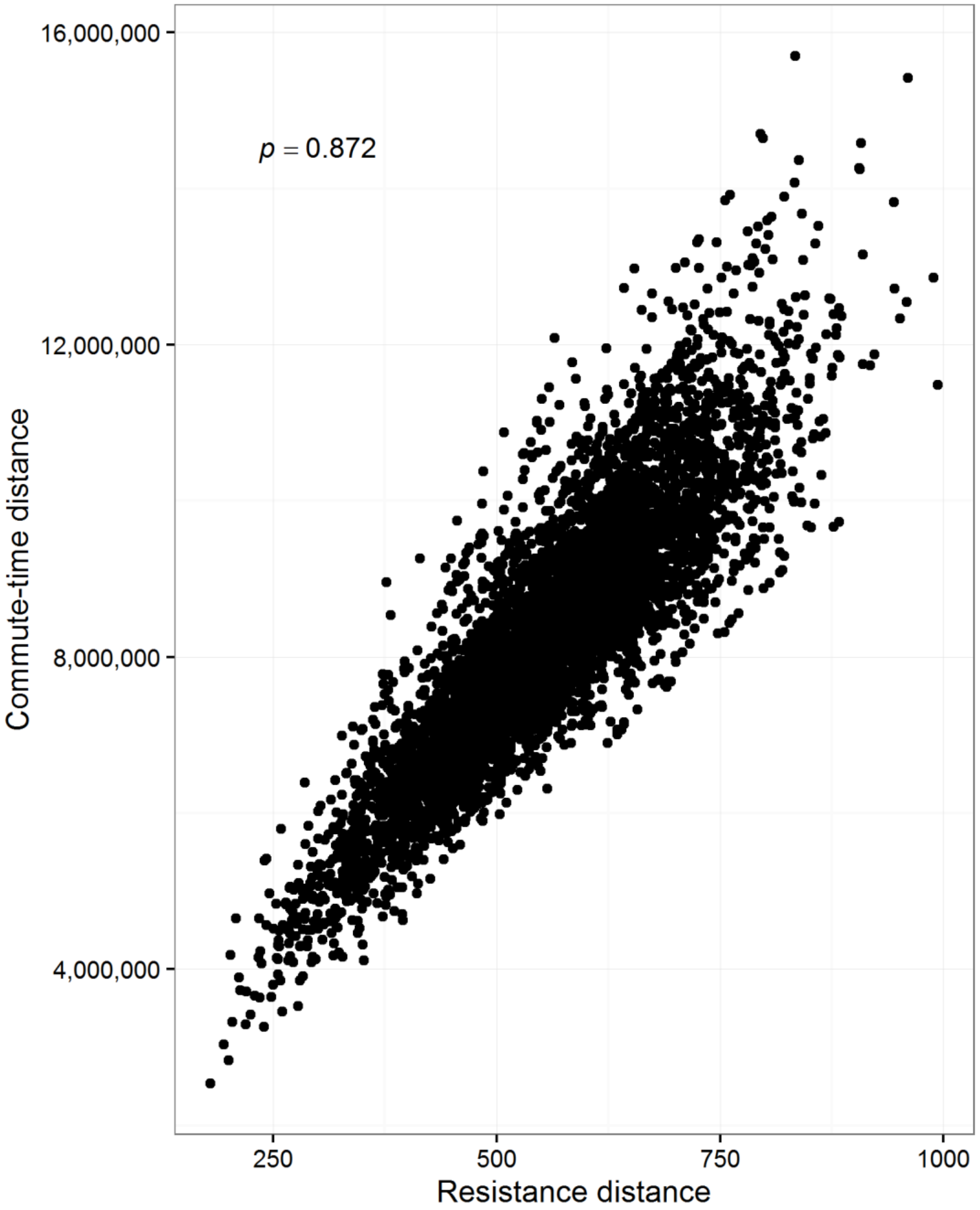

Figure S4. The relationship between resistance distance from Circuitscape [2] and commute-time from the R package gdistance [48] for a subset of 5,000 random pairs sampled from 1000 different simulated landscapes. The average Spearman's rank correlation between resistance distance and commute-time for pairwise measure between 15 randomly placed focal points on 1000 generated landscapes was 0.99 (σ = 0.00005). Landscape size (number of pixels) is held constant at 1,000,000.

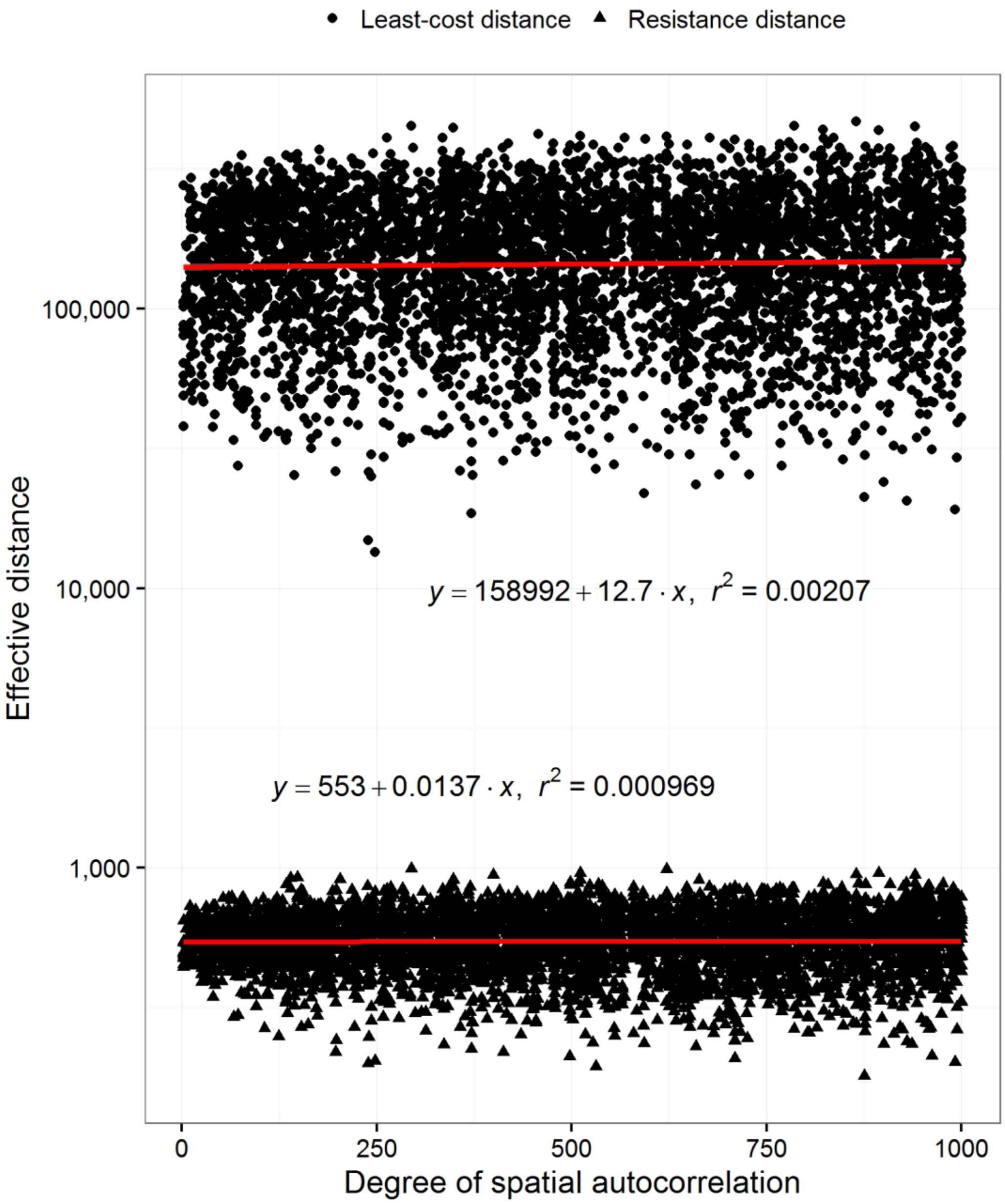

Figure S5. The effect of spatial autocorrelation. The relationship between least-cost and resistance distance and the degree of spatial autocorrelation for a subset of 5,000 random pairs sampled from 1000 different simulated landscapes. The y-axis in this graph is on a logarithmic scale for comparison purposes only. Landscape size (number of pixels) is held constant at 1,000,000.

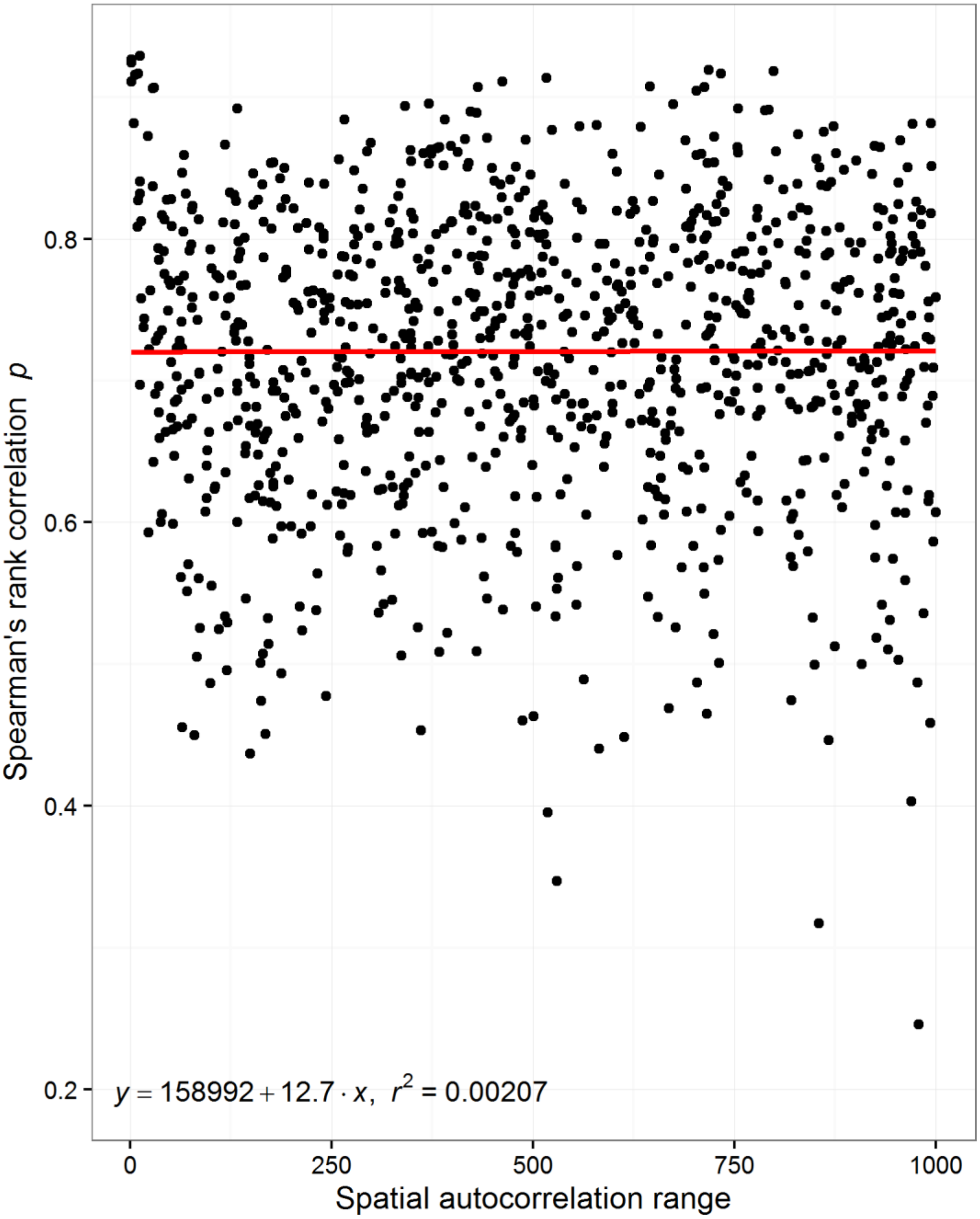

Figure S6. Spatial autocorrelation and rank order agreement. The association between least-cost and resistance distance for pairwise measurements of 15 pairwise focal points on 1000 generated landscapes with varying degrees of spatial autocorrelation. The range of spatial autocorrelation of a landscape does not affect the association between least-cost and resistance distance. Landscape size (number of pixels) is held constant at 1,000,000.

Chapter 5: Climate connectivity of the bobcat in the Great Lakes Region

Authors: Robby R. Marrotte, Jeff Bowman and Paul J. Wilson

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Contributions: RRM and JB conceived the study; RRM, JB, and PJW collected the samples; RRM wrote code, ran simulations, analyzed the data, and wrote the manuscript; JB and PJW critically reviewed the manuscript.

Abstract

The Great Lakes and the St. Lawrence River are imposing barriers for wildlife and the additive effect of urban and agricultural development that dominates the lower Great Lakes Region likely further reduces functional connectivity for many terrestrial species. As the climate warms species will need to track climate across these barriers. It is important, therefore, to investigate land cover and bioclimatic hypotheses that may explain the northward expansion of species through the Great Lakes. We investigated the functional connectivity of a vagile generalist, the bobcat, as a representative generalist forest species common to the region. We genotyped tissue samples collected across the region at 14 microsatellite loci and compared different landscape hypotheses that might explain the observed gene flow or functional connectivity. We found that the Great Lakes and the additive influence of forest stands with either low or high canopy cover and deep lake-effect snow have disrupted gene flow, whereas intermediate forest cover has facilitated gene flow. Functional connectivity in southern Ontario is relatively low and was limited in part by the low amount of forest cover. Pathways across the Great Lakes were through the Niagara region and through the Lower Peninsula of Michigan over the Straits of Mackinac and the St. Mary's River. These pathways are important routes for bobcat range expansion north of the Great Lakes and are also likely pathways that many other mobile habitat generalists must navigate to track the changing climate. The extent to which species can navigate these routes will be important for determining the future biodiversity of areas north of the Great Lakes.

Introduction

Climate is a dominant driver of species range expansion and contraction (Davis & Shaw 2001; Huntley 1999; Woodward & Williams 1987); as a result, the warming climate will inevitably shift the range of many species (Bellard *et al.* 2012; Thomas *et al.* 2004). In fact, we have already witnessed climate-induced range shifts of numerous species (Chen *et al.* 2011; Hickling *et al.* 2006; Laliberte & Ripple 2004; Parmesan 2006). Many species can adapt and persist within their original range (Bellard *et al.* 2012; Durant *et al.* 2007; Gardner et al 2009), but other species that face geographic barriers and cannot keep pace with the velocity of climate change might risk extinction (Thomas *et al.* 2004).

The ability of a species to track the changing climate by shifting its range depends in part on its niche requirements, habitat availability and connectivity (Leroux *et al.* 2013; Robillard *et al.* 2015). If a species is not able to adapt to local changes, its persistence depends on the degree to which the landscape promotes or hinders the dispersal of individuals (Fahrig & Merriam 1985; Fahrig & Paloheimo 1988; Taylor *et al.* 2006). A species' dispersal capability might depend on its physiological limitations (Travis *et al.* 2013), its demography (Clark *et al.* 2017), or its behavior (Ehrlich 1961; Pusey 1987; Warren *et al.* 2001). Large physical barriers such as mountains, oceans, lakes, and rivers can impede movement of individuals, disrupting gene flow (Grant & Grant 2009; Koen *et al.* 2015; Stebbins 1949; Steeves *et al.* 2003).

Many highly mobile species might indeed be able to track contemporary climate change across natural landforms, but the addition of cities, highways, roads and agricultural crops can potentially hinder mobility in an additive fashion (Epps *et al.* 2005; Riley *et al.* 2006; Robillard *et al.* 2015). Furthermore, suitable habitat might be found several hundreds of kilometers north of a species' current range, but the environmental characteristics of the interstitial landscape could be well outside of its niche breadth (Early & Sax 2011). In such a case the environment might impede or block dispersal and the colonization of newly available habitat (McRae 2006; Wang & Bradburd 2014). Ultimately, future biodiversity across the globe will depend on the ability of species to rapidly disperse throughout continental-scale habitat networks to keep up with changing environmental conditions. Many animals will need to migrate across human dominated and highly modified landscapes to colonize new habitats. It is therefore necessary to understand the effect that natural and anthropogenic barriers have on a species dispersal ability and to understand how these barriers influence connectivity across entire regions.

Continent-wide range expansion pathways are usually inferred from stationary biological information (estimates of dispersal distance and niche requirements) and rarely from observed patterns of movement (*e.g.*, Bagchi *et al.* 2018; Krosby *et al.* 2018; Lawler *et al.* 2013; McGuire, Lawler *et al.* 2016; Zhang *et al.* 2019). Past population dynamics are imprinted in the genes of these species (Fordham *et al.* 2014; Kawecki 2008). Such patterns have been observed in many species in the context of range change (*e.g.*, Greenhorn *et al.* 2018; Koen *et al.* 2014a; Sivyer *et al.* 2018; Zakharov & Hellmann 2008).

The Great Lakes are visibly the largest natural barrier to terrestrial species migration in eastern North America. Currently we do not know for many species, and to what extent, the Great Lakes have influenced movement and consequently gene flow, although the impacts are likely profound; much smaller barriers such as canals, highways, mountains, rivers, roads, sea lochs, and urban development have been shown to restrict the gene flow of many terrestrial vagile species (Blanchong *et al.* 2008; Coulon *et al.* 2006; Cushman & Lewis 2010; Epps *et al.* 2005; Koen *et al.* 2015; Kuehn *et al.* 2007; Pérez-Espona *et al.* 2008; Proctor *et al.* 2005; Riley *et al.* 2006; Robinson *et al.* 2013; Robinson *et al.* 2012; Vander Wal *et al.* 2012). Unfortunately, the additive influence of anthropogenic disturbance between and within the vicinity of the Great Lakes will likely further restrict gene flow through these large natural barriers for many species.

The bobcat (*Lynx rufus*) is the most widely distributed feline species in North America and there is evidence that it was more abundant across the continent before European colonization and during the Pleistocene (Deems & Pursley 1983; Graham & Lundelius 2010; Lariviere & Walton 1997). It is generally thought that intensive trapping and land clearing led to the extirpation of the species in the Midwestern United States and many parts of the Great Lakes Region and this may also have caused the apparent absence of the species in the corn belt of the United States (de Vos 1964; Deems & Pursley 1978; Deems & Pursley 1983; Woolf & Hubert 1998).

In recent decades, bobcat sightings, road deaths, and individuals incidentally harvested by trappers have become more common in the Great Lakes region (Marrotte *et al.* In Press; Roberts & Crimmins 2010; Woolf & Hubert 1998). There is evidence that bobcat populations are recolonizing into areas where they were thought to be extirpated (Linde *et al.* 2012; Woolf & Hubert Jr. 1998). For example, incidental trapper records indicate that the bobcat range is expanding north into the Rainy River district in Ontario, Canada from Minnesota and from the Upper Peninsula of Michigan (UPM) to the north shore of Lake Huron in Ontario.

However, bobcats are not spreading to the same extent into southern Ontario even though they once inhabited this landscape (de Vos 1964). Landscape configuration could be playing an important role in structuring the recolonization of the bobcat in the Great Lakes region. For instance, the Great Lakes and the St-Lawrence River are imposing barriers to movement for wildlife. In addition, urban and agricultural development dominates southern Ontario and may be impeding bobcat from colonizing this range frontier, over and above the barrier effect of the Great Lakes. There is evidence however, that the bobcat can cope in an anthropogenic environment (Lee *et al.* 2012; Riley *et al.* 2003; Tigas *et al.* 2002; Woolf *et al.* 2000). For example, in Illinois, the bobcat occupies landscapes with intensive agriculture (Woolf *et al.* 2000). It also seems capable of occupying areas surrounded by transportation infrastructure and urban development (Lee *et al.* 2012; Riley *et al.* 2003; Tigas *et al.* 2002). However, urban land cover and major highways have caused reduced gene flow in bobcat populations in California (Kozakiewicz *et al.* 2019; Lee *et al.* 2012).

Snow is also considered by some to be a limiting factor to bobcat expansion north of its range, as many researchers have suggested that the species has high foot loading and cannot efficiently travel and hunt in deep snow (Hoving *et al.* 2003; Marston 1942; McCord 1974; Parker *et al.* 1983). For example, McCord (1974) found that the bobcat had a difficult time traveling through areas that had a sinking depth exceeding 15 cm. Also, Parker *et al.* (1983) suggested that the reason the bobcat did not invade the highlands of Cape Breton was because of the deeper snow. In addition, snow clearing and compaction near human settlements may mediate the influence of snow on colonization and may promote bobcats from occupying areas north of their range (Marrotte *et al.* In Press).

We investigated several land cover and bioclimatic hypotheses that may explain the northward expansion of the bobcat throughout the Great Lakes region in North America, because any restrictions imposed on a highly mobile species would likely be even more perilous for less vagile species. We hypothesized that if there are barriers that hinder northward expansion, then we would expect less gene flow into areas of potential expansion. We considered that there are 3 scenarios that may describe range expansion in the Great Lakes Region:

H_0) Panmixia: natural and anthropogenic barriers have no effect on gene flow, thus individuals are panmictic.

H_1) Isolation by distance (IBD): natural and anthropogenic barriers have no effect on gene flow, but gene flow decays over geographic distance.

H_2) Isolation by resistance (IBR): natural and anthropogenic barriers constrict gene flow, thus flow percolates through land bridges between the lakes.

The bobcat is an ideal study species to test our hypotheses of range expansion in the context of anthropogenic change, because it is a vagile habitat generalist that is currently expanding its range and demonstrates some limitations to human disturbance and climate. We predicted that gene flow of the bobcat is obstructed naturally by the Great Lakes and deep snow but also hindered by low forest cover and by the transportation infrastructure. This model most closely follows the Isolation by Resistance hypothesis (H_2) previously described. Therefore, we predicted that gene flow is constricted through certain pathways that connect individuals throughout the region (Figure 5.1). We predicted that gene flow in southern Ontario originated mostly from the east from the province of Quebec and New York State, since flow is limited through the Lower Peninsula of Michigan (LPM) and between Lake Ontario and Erie, because of the high road density and low forest cover of these regions. On the other hand, northern Ontario is connected to the south by a more natural landscape with high forest cover and less human disturbance. Consequently, gene flow to northern Ontario is facilitated by the Upper Peninsula of Michigan (UPM) and the largely forested area to the west of Lake Superior. Our rationale is that range expansion in this region is restricted by the additive effect of natural and anthropogenic barriers. Gene flow should be constricted and forced to pass through land in between and around the Great Lakes, while deep snow should reduce the capability of flow northwards and cause gene flow to deviate around areas that receive high annual snow fall caused by the lake-effect (Norton & Bolsenga 1993). The upper Great Lakes are periodically hit by frequent lake-effect snowfall or snow squalls with over 15 cm of snow accumulation in a single day (Baijnath-Rodino & Duguay 2018). In addition, gene flow should be hindered by agricultural areas with low cover such as the corn-belt areas of the Midwest and areas with high density of roads such as urban areas.

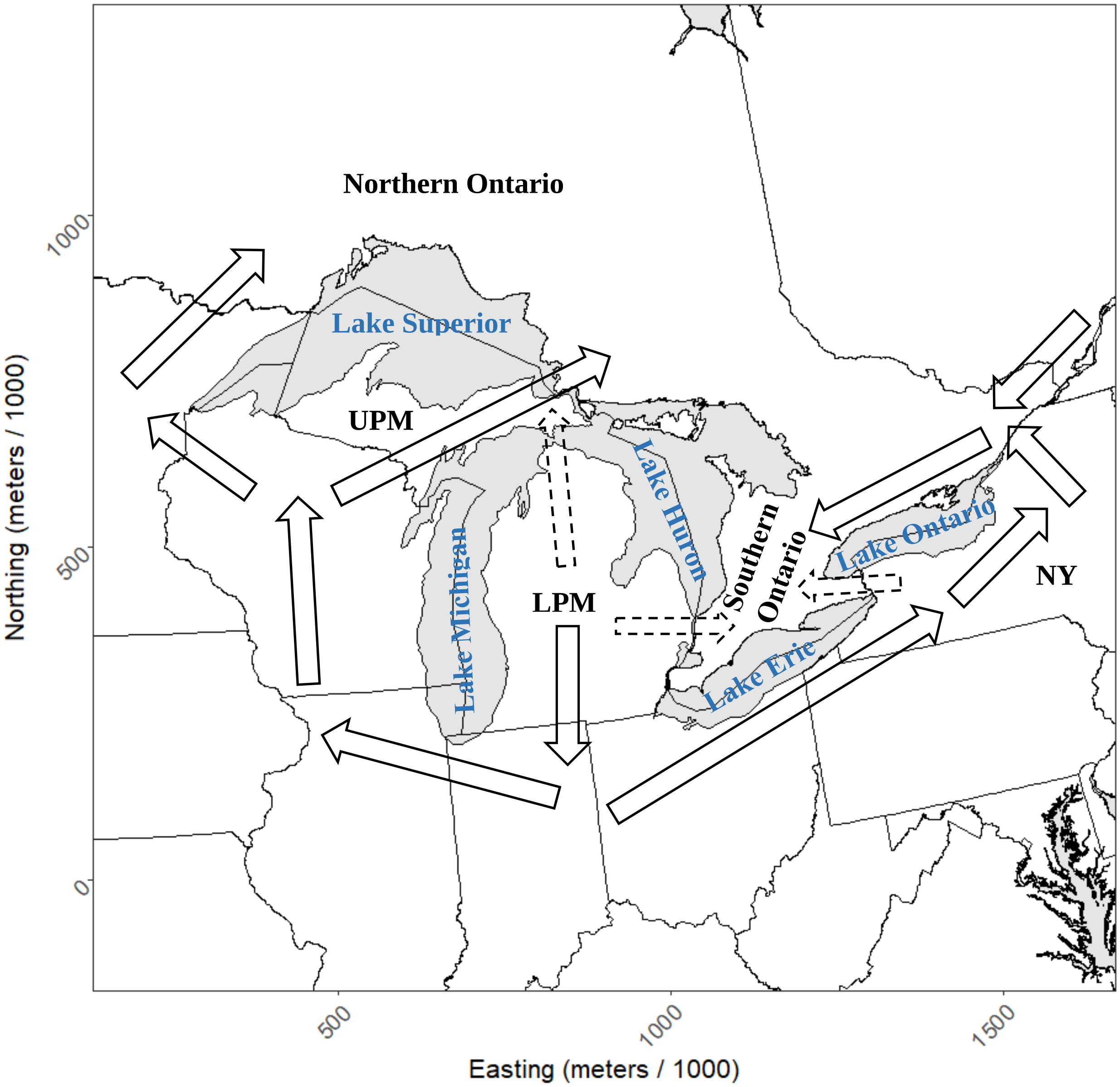

Figure 5.1. Predictions of northward expansion of a vagile habitat generalist across the Great Lakes Region in Canada and the United States. NY New York State, USA; LPM Lower Peninsula of Michigan, USA; UPM Upper Peninsula of Michigan, USA. Spatial layers for administrative

boundaries were gathered from the Database of Global Administrative Areas (https://gadm.org/). Arrows are expected to be major gene flow pathways and dashed arrows indicate areas where gene flow is thought to be constricted.

Material and Methods

Study area

From 2012 to the end of 2017, we collected bobcat pelt samples from the North American Fur Auction, Ontario Ministry of Natural Resources and Forestry, researchers, and trappers (Figure 5.2). We sampled bobcat pelts found within an area around the Great Lakes defined by the maximum dispersal distance of the bobcat of 300 km (Johnson *et al.* 2010). We sampled on both sides of the international border between Canada and the USA.

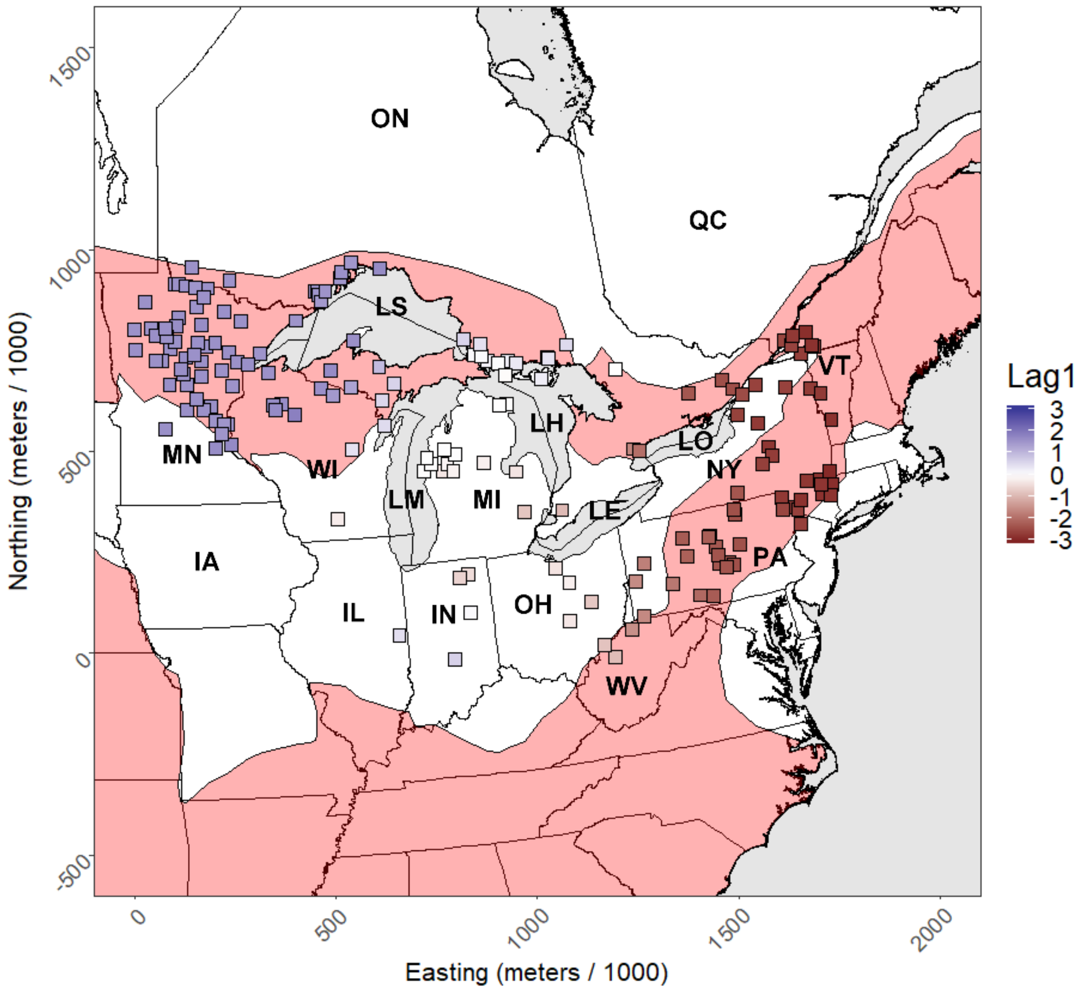

Figure 5.2. Location of 240 bobcat (Lynx rufus) fur samples collected from a variety of sources between 2012-2017 across the Great Lakes region in Canada and the United States. The shaded area is the consensus bobcat range according to the IUCN and the Nature Conservancy. Lag1 is the first axis from a spatial principal component analysis on the alleles scores of bobcats. It represents the only significant major spatial variation across bobcats in the Great Lakes region. Labels are: ON Ontario, Canada; QC Quebec, Canada; MN Minnesota, USA; WI Wisconsin, USA; MI Michigan, USA; NY New York, USA; VT Vermont, USA; IA Iowa, USA; IN Indiana, USA; OH Ohio, USA; PA Pennsylvania, USA; WV West Virginia; LS Lake Superior, LM Lake Michigan; LH Lake Huron; LE Lake Erie; LO Lake Ontario.

Genetic analysis

We followed the lab protocols and scoring methodology of Koen *et al.* (2014a) and Row *et al.* (2012) and genotyped bobcat samples at 14 microsatellite loci (Fca031, Fca035, Fca043, Fca077, Fca090, Fca096, Fca441, Fca391, Fca559, Lc106, Lc109, Lc110, Lc111, Lc118). We removed individuals that had any missing loci and individuals that were not correctly georeferenced.

We then explored the spatial structure of these data using a spatial principal component analysis (sPCA; Jombart *et al.* 2008) and tested for patterns of spatial autocorrelation. We used a distance-based nearest neighbour approach, where individuals within 300 km were assumed to be neighbours, since bobcat have been observed to disperse up to 288 km from their natal range (Johnson *et al.* 2010; Knick & Bailey 2006). We also tested different neighbourhood approaches and found similar spatial patterns. We used a Monte Carlo global test to determine whether there was any global or local spatial structure worth investigating (Jombart 2008). We permuted the alleles scores 9999 times to test the significance of the spatial structure. If there was no spatial structure, then the panmixia hypothesis (H_0) would be concluded, because our Isolation by Distance (H_1) and Isolation by Resistance (H_2) hypotheses were inherently spatial. After exploring the spatial structure, we then used the proportion of shared alleles as a metric of genetic similarity between individuals and tested our spatial hypotheses.

Gene flow covariates

We built 4 different landscape maps which we thought could explain bobcat gene flow in the Great Lakes region, and that would allow us to test our Isolation by Resistance hypothesis (Figure 5.3). To establish the spatial extent of our analysis we used the minimum convex hull that contained the Great Lakes with a 400 km buffer to leave 100 km between the edge of the map and any bobcat samples (Koen *et al.* 2010). The Great Lakes spatial layer we used to create this boundary and the St-Lawrence river layer that we later used were gathered from the Lakes and Rivers, 2009 spatial layers freely available by the Commission for Environmental Cooperation (CEC; cec.org).

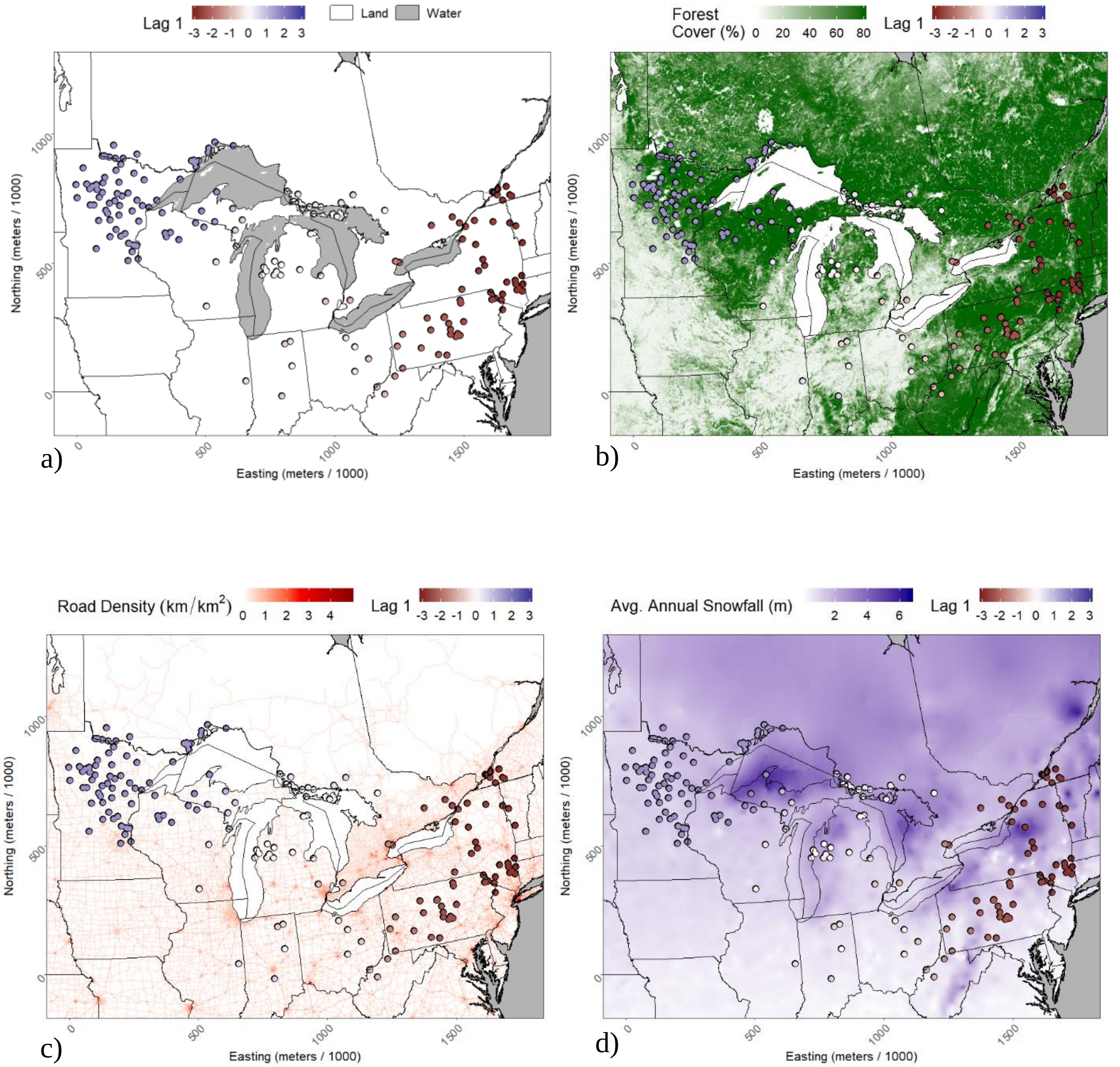

Figure 5.3. Landscape maps used to test Isolation by Resistance hypotheses of bobcat gene flow across the Great Lakes region. a) Great Lake barrier, b) Forest cover, c) Road density, and d) Annual snow fall. In total 8 Isolation by Resistance models were tested and included only combinations of the Great Lakes model with all other 3 landscapes. We also compared these models to a null model of panmixia (H_0) and an Isolation by Distance (H_1).

To create our Great Lakes landscape layer, we assigned values of 1 to areas where there was either the Great Lakes or the St-Lawrence and the value 2 to the land (Figure 5.3a).

We used the forest cover layer provided by the University of Maryland, which has a continuous forest cover field where each pixel has an assigned value that represented the percentage of tree cover as the data source for our second map (glcf.umd.edu/data/treecover; DeFries *et al.* 2000). This forest cover layer extended across North America at a resolution of 1 km^2 with values that ranged from 10 to 80% forest cover. However, there were values of 254 and 255, which represented areas that were non-vegetated and areas where tree cover was less than 10%. We assigned a value of 1 to areas that were non-vegetated and a value of 5% to areas that were less than 10% vegetated (Figure 5.3b). We were not able to find tree cover at such a fine resolution that matched the temporal resolution of our bobcat data, but there has not been much recent forest loss in our study area; from 2000 to 2017, the largest forest loss was in Minnesota which had a decrease of forest cover by 6.9% (globalforestwatch.org).

We used the freely available road layer provided by Natural Earth (naturalearthdata.com) to create our next landscape. We calculated the road density within a radius of 1 km from the centre of a pixel with a resolution of 1 km (Figure 5.3c).

For our snow layer, we gathered annual data from the Global Historical Climatology Network (GHCN; ncdc.noaa.gov/snow-and-ice), which provides data tables for climate stations found across the world. We chose stations found within Canada and the United States that had more than 15 years of data between 1980 and 2011 and calculated the mean annual snow fall mean of each climate station. We then interpolated these data using ordinary spherical kriging (Figure 5.3d).

All surfaces were aggregated using the mean for continuous surfaces and the mode for discreet surfaces to a resolution of 2 km to reduce computation time. We masked out the ocean using a landform layer also provided by Natural Earth. All our layers were projected to North America Lambert Conformal Conic (https://epsg.io/102009).

Statistical framework

Our hypotheses were that bobcat gene flow across the Great Lakes Region is panmictic (H_0), a function of distance (H_1), or a function of resistance (H_2). Therefore, we first investigated 2 models that simply tested for panmixia and Isolation by Distance, and we then tested 8 Isolation by Resistance models that combined landscape features (Table 5.1). The Great Lakes barrier was present in all 8 landscape models. We did not find it logical to test Isolation by Resistance models in the absence of the Great Lakes, because forest cover, road density and snow cover are additive effects on gene flow and not solitary effects. We reasoned that bobcats cannot inhabit a lake but could occupy an area where there is no forest cover, high road density and deep snow. Also, these Isolation by Resistance models included the influence of Isolation by Distance, because of the nature of resistance distance (McRae 2006).

For each hypothesis we fit the proportion of shared alleles using Generalized Linear Mixed Models with a normal error structure and a ‘log’ link, since we reasoned that the influence of landscape features on gene flow decays exponentially across space. We also found higher variance explained using an exponential model compared to a linear model. We used a maximum-likelihood population-effects covariance structure to account for the non-independence of the pairwise nature of the data (Clarke *et al.* 2002). For our Isolation by Resistance models, we were interested in estimating the resistance of the landscape, consequently, we used landscape resistance optimization using circuit theory (Marrotte *et al.* 2014; McRae 2006; Peterman 2018). We optimized the resistance of each landscape map with the functions provided in the “ResistanceGA” package (Peterman, 2018) but did not modify any genetic algorithm parameters. We used Circuitscape v.5.3.0 (Anantharaman *et al.* 2019) in the Julia language v.0.6.2 (Bezanson *et al.* 2012) to calculate the effective distance between individuals (Anantharaman *et al.* 2019). We fit all mixed effects models with the package "lme4" (Bates *et al.* 2014) in R v.3.5.1 (R Development Core Team 2018).

We also accounted for uneven sampling intensity, because it could lead to sampling artifacts (*e.g.,* Kierepka & Latch 2016) and eventually spurious conclusions if overlooked (Balkenhol & Fortin 2015). Consequently, we resampled the individuals with replacement into 999 sets of individuals that were at least 100 km apart across the study area. We chose a minimum distance of 100 km, because it gave us the ability to homogenize sampling intensity across the study area and gave us a larger number of individuals to investigate. In contrast, a larger distance would have left us with less than 30 individuals and a smaller distance would have left us with quite variable sampling intensity across the study area (Figure 5.2). In addition, resampling gave us the ability to replicate our models on 999 different combinations of data, therefore gave us the ability to measure the consistency of our results. Given the computation time required to optimize the resistance surfaces and the large number of replicates (7992), we fit our models using several computer clusters (Cedar, Graham and Orca; computecanada.ca).

We finally ranked each model within its set of replicates with AICc. We also calculated the overall average rank, AICc, ΔAICc and $AICcW_t$ to compare each model. We then used a Branch-and-Bound algorithm in R to find the consensus median ranking of all 10 models using the "ConsRank" package (D'Ambrosio *et al.* 2015).

Functional Connectivity

By Ohm's Law, circuit resistance is reciprocal to current. Fundamental work in genetics by McRae (2006) demonstrated that current is proportional to gene flow (McRae 2006). To help answer our research question concerning how bobcat populations are connected through the Great Lakes Region, we then created an omnidirectional current density map. We gathered all 999 optimized resistance surfaces of the top landscape model and for each surface we first standardized the optimized resistance to the mean. We then calculated the average resistance of each pixel to produce a map of standard average resistance (resistance from this point forward). We then used circuit theory in Circuitscape version 4.05 to produce a current density map (Shah & McRae 2008). We generally followed the methods of Koen *et al.* (2014b) to produce an omnidirectional current density map. However, resistance values cannot be negative; therefore, we first scaled the values between 1 and 100. We then regularly placed 100 nodes at the periphery of the map and simulated current passing between all pairs and summed the total current passing through the Great Lakes Region. In conjunction with the optimized average standard resistance surface, this current map gave us an idea where current or gene flow was being restricted or impeded.

Results

We used 240 samples after removing those with missing alleles, that were not accurately georeferenced, or that were outside our delineated study area (Figure 5.2). The low number of samples within some US states was a result of the status of legal hunting or trapping or the low abundance of the bobcat. For example, in 2016 the state of Illinois opened the bobcat season after 40 years of being closed, so we were only able to collect a single pelt sample from this US state. In Indiana, we were only able to collect 4 bobcat pelt samples, because hunting and trapping has been closed since 1969.

After performing an sPCA on the allele scores, we found 1 significant pattern (Observation: 0.020, p-value: 0.001, Figure 5.2). There was a NE to NW pattern in bobcat allele scores across the Great Lakes Region, where individuals in both northern corners of the Great Lakes Region were found at opposite ends of this gradient.

The proportion of shared alleles ranged from 0.07 to 0.63. All 999 sets of samples had on average 37 individuals and ranged from 31 to 43 individuals. Due to the way we bootstrapped our samples, some samples were selected more often than others. On average individuals were sampled 154 times and this ranged from 2 to 999 times. There were only 3 samples (from Indiana, Illinois, and Ontario) that were sampled in every set. The 3 individuals were sampled each time, because they were isolated in an area more than 100 km from the nearest other individuals. We checked whether the 3 samples might have driven the optimization of the resistance surface and we found that the resistance values within 100 km of each of these sites were near the average range compared to other areas on the map (0.17, 0.38 and 0.23). Only 1 individual was sampled as little as twice; this sample was in the highly sampled area in western Minnesota.

The composite landscape model that generally ranked first with AICc within its set using the consensus Branch-and-Bound algorithm, included the Great Lakes, forest cover, and annual snowfall (Table 5.1). In addition, this composite landscape model had the lowest average rank, AICc and ΔAICc. This composite model ranked first 19.2%, second 22.1%, and third 16.5% of the time, and had the largest proportion of its replicates in the top 3 ranks, but the Great Lakes and Forest cover model did have more replicates that ranked first (22.2%; Table 5.1). The marginal R^2 for the top composite landscape model had a mean of 0.332 [0.079,0.690] with a conditional R^2 with a mean of 0.655 [0.446,0.881]. All other models did not rank better than the Isolation by Distance model. In comparison, this model had an average marginal R^2 of 0.106 [0,0.362] with a conditional R^2 of 0.545 [0.334,0.759]. This indicated that gene flow was a function of geographic distance, and additionally gene flow was restricted by the Great Lakes, forest cover, and snow over our study area.

*Table 5.1. Summary statistics for 10 landscape models used to explain bobcat gene flow in the Great Lake Region. Consensus rank was determined using the AICc between the 10 models within each 999 set of replicates. Values in bold font are the best value of each metric. All models except the panmixia (H_0) and Isolation by Distance (H_1) were Isolation by Resistance models (H_2). * Great Lakes.*

Model	**Consensus Rank**	**Average**						**Rank Percentage**		
		AICc	**R^2m**	**R^2c**	**Rank**	**ΔAICc**	**ω_i**	**1st**	**2nd**	**3rd**
GL* + Forest + Snow	1	**-1419.60**	0.33	**0.66**	**3.84**	**9.21**	0.20	19.22	**22.12**	**16.52**
Isolation by Distance	2	-1414.24	0.11	0.55	4.20	14.57	0.17	18.82	11.51	10.61
GL + Forest	3	-1416.79	0.25	0.62	4.26	12.02	**0.22**	**22.22**	13.11	9.91
GL + Snow	4	-1415.22	0.25	0.62	4.64	13.59	0.15	15.42	10.51	11.01
GL + Roads	5	-1412.28	0.23	0.60	5.36	16.53	0.08	8.41	9.61	6.51
GL + Roads + Snow	6	-1414.00	0.30	0.64	5.31	14.81	0.11	10.21	12.81	11.71
GL	7	-1409.33	0.13	0.56	5.91	19.48	0.04	3.10	8.41	9.81
GL + Forest + Roads	8	-1411.29	0.29	0.63	6.11	17.52	0.02	2.20	6.41	13.91
GL + Forest + Roads + Snow	9	-1406.65	**0.34**	**0.66**	7.32	22.16	0.00	0.20	2.60	5.71
Panmixia	10	-1399.75	0.00	0.49	8.05	29.06	0.01	0.20	2.90	4.30

Summary statistics from the resistance optimization algorithm allowed us to determine how much each covariate contributed to the optimized resistance surface (Peterman 2018). We found that the contribution of the forest cover was the highest (μ = 58.5%), followed by snow (μ =

37.8%) and then the Great Lakes barrier (μ = 3.7%). The mean slope of this model was -0.079, with only 6 of 999 iterations having a positive slope. Thus, in most cases, the effective resistance was positively correlated with genetic distance.

After scaling all replicates of the optimized surfaces of the best combined landscape model and taking the average through each pixel we found that the Great Lakes had a higher resistance compared to other features on the landscape (Figure 5.4-5). In fact, the resistance values in the Great Lakes were on average 1.557 [0.579,2.104] times higher than the rest of the landscape. Generally, areas with low and high forest cover had high resistance values, whereas intermediate values that neared 60% forest cover had the lowest values (Figure 5.4a). This pattern was also the same for annual snow fall (Figure 5.4b), areas with low and high annual snow fall had high resistance compared to areas with intermediate annual snow fall that neared 2 meters of annual snow fall.

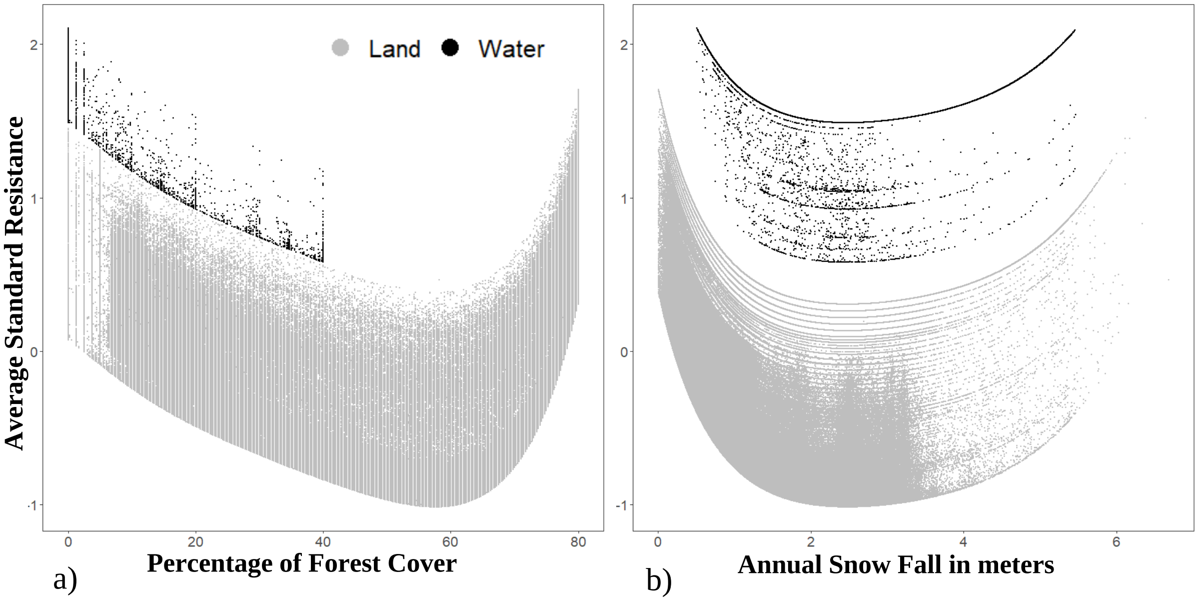

Figure 5.4. Optimized average standard resistance transformation. a) Forest cover optimized resistance transformation. In some shoreline areas forest cover overlapped the Great Lakes layer and values were optimized as if they were the Great Lakes land barrier, therefore these shoreline areas received high average standard resistance simply because of the mismatch

between spatial layers. However, in the interior, intermediate forest cover around 60% amplifies gene flow while low and high forest cover impedes gene flow, but high cover impeded gene flow more over the Great Lakes Region. b) Annual snowfall optimized resistance transformation. Annual snowfall on the lakes was generally transformed to high resistance values compared to land. On land, low annual snowfall impeded gene flow the most, while high annual snow usually found in lake-effect areas also impeded gene flow. Like forest cover, intermediate amounts of annual snowfall amplified gene flow over the Great Lakes Region.

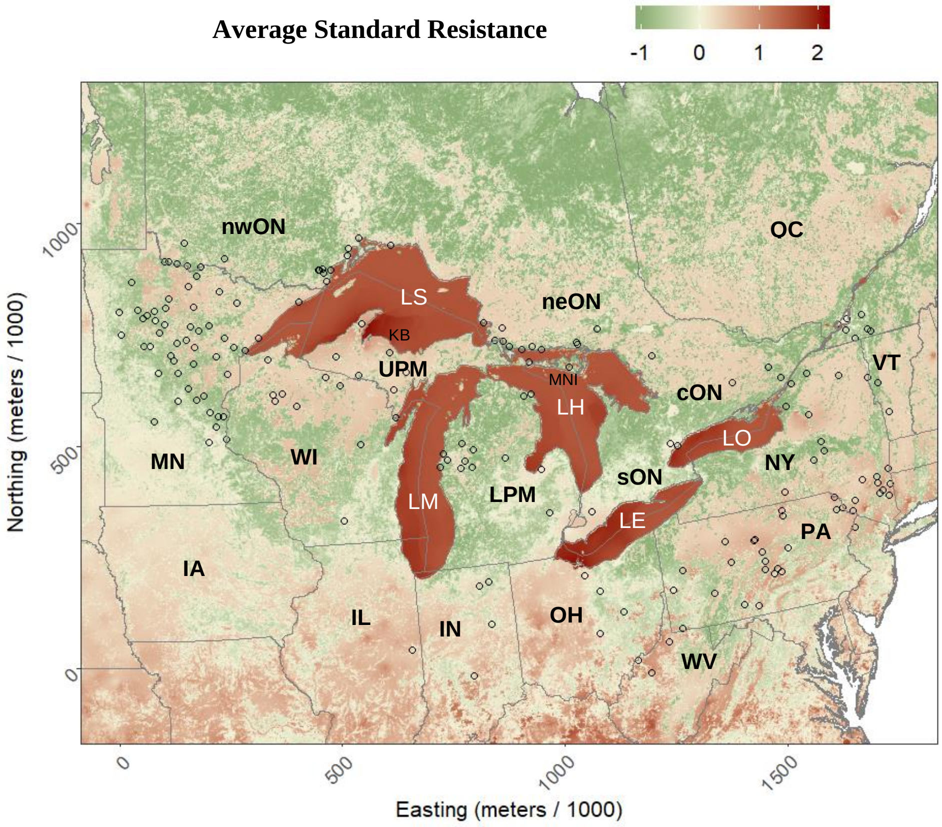

Figure 5.5. The average standard resistance from 999 replicates of the top model that was fit using resistance surface optimization of a landscape model that included the additive effect of the Great Lakes, forest cover and annual snow fall. These models were fit to the genetic similarity of bobcat samples across the study area. Labels are: nwON northwestern Ontario, Canada; neON northeastern Ontario, Canada; cON central Ontario, Canada; sON southern Ontario, Canada; QC Quebec, Canada; MN Minnesota, USA; WI Wisconsin, USA; UPM Upper Peninsula of Michigan, USA; LPM Lower Peninsula of Michigan, USA; NY New York, USA; VT Vermont, USA; IA Iowa, USA; IN Indiana, USA; OH Ohio, USA; PA Pennsylvania, USA; WV West Virginia; LS Lake Superior, LM Lake Michigan; LH Lake Huron; LE Lake Erie; LO Lake Ontario; KB Keweenaw Bay; MNI Manitoulin Island, Ontario, Canada.

There were generally spatial patterns of resistance and current density over our study area. For instance, resistance was high in the lower Great Lake states, but there was a zone of low resistance that overlapped Pennsylvania and Ohio (Figure 5.5). Conversely, resistance was lower in the upper Great Lake States and farther south. Though resistance seemed high in New York State, there was an "L" shaped corridor of low resistance and high current that followed the border between Vermont and New York State from the border of Quebec and turned west from the tristate boundary and continued all the way to the Canada and USA border between Lake Ontario and Lake Erie. This area with low resistance connected QC, VT and NY State with a square corridor around the Adirondack region (Figure 5.6). This corridor also connected to southern Ontario and jumped the St-Lawrence river from the Thousand Islands Archipelago between Canada and the United States into Ontario.

On the Lower Peninsula of Michigan (LPM) resistance was low and current was high compared the Upper Peninsula. The high resistance and low current area of the UPM also overlapped to some extent northern Wisconsin and northeastern Minnesota. In southern Ontario, Canada, resistance was high and decreased into central Ontario but increased once again towards northeastern Ontario. The current mimicked this pattern but was also amplified on the Niagara Escarpment. On the shores of Lake Huron resistance was low and current high, and this was also true for Manitoulin Island. Comparatively northwestern Ontario had low resistance and consequently high current. Other important corridors were the high current areas that followed Mississippi river into Manitoba and northern Ontario and the pinch point that connected Michigan to northern Ontario from the Straits of Mackinac.

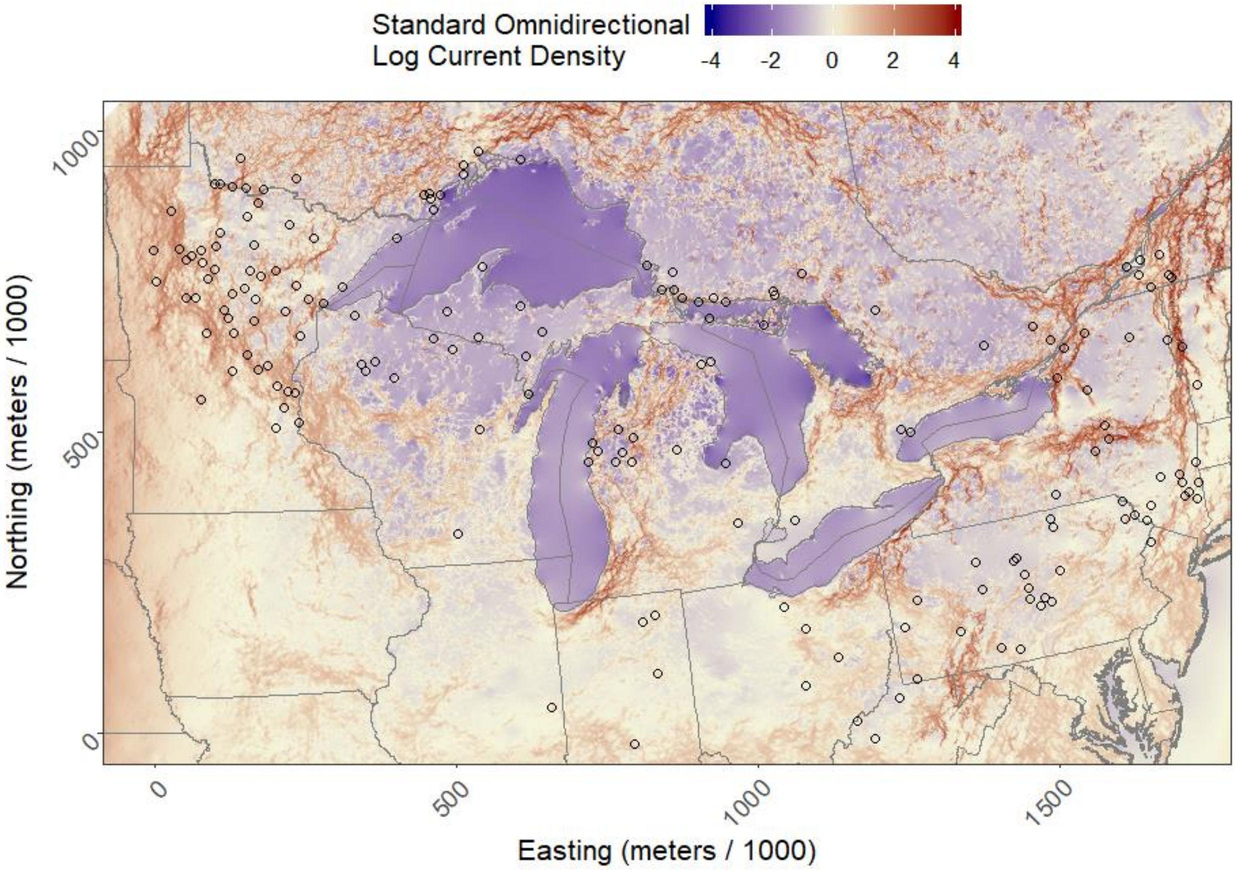

Figure 5.6. Current density for gene flow through the Great Lakes Region. Current density was estimated from the pairwise current of 100 nodes placed on the extremity of all sides of the study area. We used the average standard resistance surface of the top model and rescaled the values from 1 to 100 and used Circuitscape to calculate the cumulative current density of the pairwise iteration of the 100 nodes. We then standardized and scaled the current density to the mean. A value of 0 indicates areas that have average current density and values less and greater than 0 indicate below and above average current density.

Discussion

We originally hypothesized that bobcat gene flow percolated between the Great Lakes and deep snow areas but was also hindered by low forest cover and by the transportation infrastructure. We found significant spatial structure where gene flow was constricted by the Great Lakes and areas with low and high forest cover with deep lake-effect snow, while intermediate forest cover facilitated gene flow in the Great Lakes Region. Although we did not anticipate the bimodal effect of forest cover, our findings were consistent with our Isolation by Resistance hypothesis (H_2).

The warming climate will only aid in the expansion of vagile habitat generalists, since areas of deep lake-effect snow may eventually disappear. However, the Great Lakes and areas with low forest cover limited gene flow more than snow, therefore, we can only predict that less mobile and generalist species will have a more difficult time spreading northward across this landscape as they track climate. In addition, connectivity will be further restricted if these species are not resilient to disturbance such as road, highways and urban development. Our results are in accordance with a previous analysis that estimated the margin of success of species ability to track climate between natural regions across the United States. The authors found that the network of habitat patches of the Great Lakes Region largely failed at connecting habitat that species might use to track the warming climate (McGuire *et al.* 2016).

We also predicted that certain pathways connected populations throughout the region (Figure 5.1). We wrongly predicted the use of the Upper Peninsula of Michigan as a main pathway to northern Ontario but found that the Lower Peninsula was more probable. This would mean that species would be forced to cross the Straits of Mackinac and the St. Marys River. The route from the Lower Peninsula is likely treacherous to many species, since it requires the crossing of a vast 5 kilometer stretch of water, or ice in the winter months. The latter will become less common as the climate warms. It is also likely that the UPM will be favored as climate warms, since deep lake-effect snow will become less likely and this route also does not require crossing a 5 kilometer stretch of water. However, both the LPM and UPM require the crossing of the St. Marys River. We also incorrectly predicted the importance of the Niagara Region pathway between Lake Ontario and Erie. However, the Niagara Region pathway might only be traversable by mobile species like the bobcat that are resilient to anthropogenic disturbances, since the area has a high density of roads compared to other pathways through the Great Lakes (Fig. 3c). For example, gene flow of the highly adaptable raccoon (*Procyon lotor*) was restricted through this route between Canada and the United States and this also matched the pattern of raccoon rabies incidences at the time (Cullingham *et al.* 2009).

Natural barriers

We found that the Great Lakes on average, had high resistance compared to any other feature on the landscape (Figures 4 and 5). Although at first glance, we did find that the Great Lake barrier itself did not contribute much to the optimized resistance values of the top models (Table 5.1), but this was due to the snow layer which created a spatial trend within the Great Lakes (Figure 5.5). The pattern within the lakes was caused by the large quantity of annual snow received due to the lake effect (Figure 5.3d). The variability in snow found within the Great Lakes seemed to be important, since models that included snow ranked better than the Great Lakes and forest cover models (Table 5.1). For example, in Keweenaw Bay in Lake Superior (KB; Figure 5.5), resistance was higher than the rest of the lake and this was due to the high amount of snow that the bay received annually due to the lake effect (Figure 5.3d).

In all, even if the Great Lakes and annual snow were confounded, the outcome was the same, the Great Lakes were without a doubt a barrier to gene flow whether it was caused by the lakes themselves as a barrier or the deep snow that accumulated on them in winter when they freeze or both. On land, snow alone did not seem to be quite important overall, but there were a few areas where the lake-effect snow was quite important, this was the UPM, the Bruce Peninsula and the area to the east of Lake Ontario that intersected some parts of the Adirondacks (Figure 5.3d). However, only the UPM and the east side of Lake Ontario had higher resistance (Figure 5.5).

Our prediction that snow restricted gene flow northward over our study area did not hold; this could have been due to the low number of samples in the more northern areas of the bobcat's distribution where snowfall is much higher (Figure 5.3d).

Gene flow into the northern range limit

Gene flow in southern Ontario was more likely through the Niagara region from New York State, since we found that the land that connected both areas was less resistant to gene flow and this was due to low forest cover (Figure 5.3b and 4). From this point, gene flow was possible into central Ontario, since resistance decreased and current increased northward. Bobcat have been reported in central Ontario in the past and occurrences are more common than in southern Ontario. In fact, bobcats were once common on the Bruce Peninsula (de Vos 1964).

Gene flow to northern Ontario was not facilitated by the UPM and the forests of western Ontario as we previously hypothesized. We found that gene flow into northern Ontario through the UPM is less likely and had more likely occurred through the LPM (Figure 5.5-6). This was a surprising result, since the UPM previously seemed more likely because of the high amount of forest cover and because the LPM was an area where the bobcat was slowly recolonizing after it was extirpated (Figure 5.2). However, considering our results the LPM is more appropriate because of the intermediate amount of forest cover which seemed to amplify gene flow (Figures 5.4-5). In addition, snowfall on the UPM was much higher than the LPM. In fact, the average annual snowfall on some areas of the UPM exceed well over 6 meters (Figure 5.3d). In contrast, the average annual snow on the LPM was shallower with depths not exceeding 4 meters, but compared to the UPM, these snowy areas occupied less of the land. Furthermore, the major thruway from the LPM to northern Ontario was across the 5.6 km long Straits of Mackinac which was only feasible in the winter when the lake was frozen. From our own experience tracking bobcats, it is not uncommon to observe bobcat that cross large bodies of water in winter. A bobcat with a GPS collar from our study crossed the North Channel to the Grant Islands, a distance > 5 km across Lake Huron ice (unpublished data).

The importance of intermediate forest cover

Even if the Great Lakes had the highest resistance, forest cover had the highest average contribution to restricting gene flow. Though, we previously thought that high tree cover would amplify gene flow, we found that intermediate amount of forest amplified gene flow. Also, forests with 80% tree cover hindered gene flow more than areas with no tree cover (Figure 5.4). One common assumption is that the bobcat is a habitat generalist (Anderson & Lovallo 2003), consequently it does not specialize on any specific habitat type across its range, therefore it may perform better in environments with an average amount of forest cover compared to area that are 0 or 80% forest cover. Areas with low forest cover are either urban centers or areas that are predominantly used for agricultural purposes. Theses areas are mostly found in the Midwest corn belt of the USA where tree cover was low over our study area (Figure 5.3b). The corn belt was first cleared for agriculture in the 1850s and since then has been an area with low biodiversity and intensive agriculture use (Jenkins *et al.* 2015; Nassauer *et al.* 2007). Compared to more forested areas, the corn belt may have lower abundance and diversity of prey species that may not be able to sustain the bobcat.

On the other extreme, areas with high forest cover, were areas where bobcat gene flow was obstructed, these forests were generally found in the upper Great Lakes region and were also found in the Appalachian corridor and the Adirondacks. Some of these forests with high amount of canopy cover also had high annual snowfall compared to other areas of the bobcat range in our study area (Figure 5.3b & d). Bobcat may not be able to effectively hunt in dense forests with high annual snow fall compared to forest with similar snow and intermediate forest cover.

The bobcat needs some forest cover to stalk prey (McCord 1974), but perhaps the forest cover cannot be so dense as to reduce visibility and muffle sound, since the bobcat relies heavily on sight and sound to hunt (McCord & Cardoza 1982), therefore forests with an intermediate amount of cover might be more preferred by bobcat. The ability to see and catch prey is a function of forest cover but also there is an interplay with snow depth, since deep snow reduces their ability to hunt (McCord 1974). To some extent forest cover was also associated to road density; in cases where road density was high, forest cover was reduced, and this happened near urban areas (Figure 5.3b-c). In more rural communities, where forest cover is intermediate with road density, bobcat gene flow was amplified.

Bobcat range expansion

In general, our results suggest that the northward expansion of the bobcat in the Great Lakes Region has been facilitated by intermediate forest cover. Therefore, the expansion of the bobcat is in part a response to the decrease in forest cover due to land clearing and forestry in the Great Lakes region. In fact, in the northern Great Lakes US states the area occupied by open land has increased from 12.3% to 41.3% since 1836 (Schulte *et al.* 2007), which is within the range of optimal forest cover for bobcat gene flow that we found in our analysis (Figure 5.4). This land clearing may have opened previously unavailable habitat in northern Ontario to bobcat, but deep winter snow may have still been a limiting factor until snow depth subsided due to climate change in later years (Dyer & Mote 2006).

After this point, further north, bobcat began to be harvested by trappers in northwestern Ontario in the early 1900s and in northeastern Ontario in the mid-1900s (de Vos 1964). The 50-year lag period between these two areas could have been due to the disparity in the amount of annual snow received in both areas (Figure 5.3d). Northwestern shores of Lake Superior received less snow than the northern shores of Lake Huron. Currently, on the north shores of Lake Huron intermediate forest cover is still important to bobcat, since bobcat in this area are almost exclusively found in rural communities within 50 km of urban centers (Marrotte *et al.* In Press). The increasing density of human disturbances such as roads, rail lines, urban areas, rangeland, and agricultural land, would have also further amplified colonization, because road plowing and snow compaction would have become more frequent which allowed bobcat to move around and hunt more effectively. Therefore, at their northern limit, areas with intermediate forest cover that have an intermediate density of roads may have mediated the colonization of bobcats into areas the bobcat generally would not have occupied, because of deep annual snow.

Overall, land use and cover change and the decreasing snowpack due to climate change will only facilitate the expansion of bobcat and we can only expect to find bobcats further north each year. However, it is important to note that the landscape of southern Ontario has impeded gene flow and consequently movement of bobcat over the past decades. As the climate continues to warm and species are tracking their bioclimatic niche through the Great Lakes Region, we can only expect that less mobile species are less likely to cross southern Ontario. Other routes are already blocked by natural features such as the St-Lawrence River, the 5.6 km Straits of Mackinac and the St-Marie`s River and the additive effect of human modification will undoubtedly further restrict these routes and reduce future potential biodiversity.

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Data Availability

The data and R scripts that support the findings of this study are openly available on Dryad at https://doi.org/10.5061/dryad.zgmsbcc6d.

Author Contributions

RRM and JB conceived the study; RRM, JB and PJW collected the samples; RRM wrote code, ran simulations, analyzed the data, and wrote the manuscript; JB and PJW critically reviewed the manuscript.

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Chapter 6: Spatial segregation and habitat partitioning of bobcat and Canada lynx

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Contributions: RRM and JB conceived the study; RRM and SJM collected data in the field; RRM wrote code, analyzed the data, and wrote the manuscript; JB and SJM critically reviewed the manuscript.

Abstract

Harvest records suggest that the abundance of bobcats (*Lynx rufus*) has increased and the leading edge of their distribution has spread northward, while the trailing edge of the Canada lynx (*Lynx canadensis*) range has contracted in Ontario, Canada. There has been a debate about whether these closely related felids might compete in areas of sympatry, but there is little research on sympatric populations of bobcat and lynx. Both species are found on the north shore of Lake Huron in Ontario, Canada, which provided an opportunity to investigate their spatial patterns and habitat use. We surveyed snowmobile routes for snow tracks over 3 winters and estimated probability of occupancy for the two felid species while accounting for detectability. Bobcat and lynx tracks were never found on the same survey route. Bobcat occupancy increased with habitat heterogeneity whereas lynx occupancy increased with homogeneity. Our results fit with the common assumption of the generalist and specialist natures of bobcat and lynx, respectively. Our findings suggest that bobcats invaded former lynx territory after these areas became vacant. The story of the bobcat and the lynx is one of the loss of a unique, boreal specialist due to anthropogenic change, and eventual replacement by an adaptable generalist.

Key-words: Spatial Segregation, Habitat Partitioning, *Lynx rufus*, *Lynx canadensis*, Occupancy, Competition.

Introduction

When resources are limiting, closely related species cannot coexist without having niche differences or undergoing some form of niche partitioning (Amarasekare 2003, Brown and Wilson 1956, MacArthur 1958). In areas of contact, the species may coexist by exploiting different dietary or habitat resources (Brown and Wilson 1956, Pfennig and Pfennig 2009) or by eluding each other in space and time (Amarasekare 2003, Armstrong and McGehee 1976, Chesson 2000). Occurrence patterns and their causes are important to investigate because they help us understand how closely related species coexist (MacArthur 1984). This is especially true as the ranges of many species are changing with the warming climate (Laliberte and Ripple 2004, Thomas 2010, Wolf and Ripple 2017). Contact zones are following suit with new ones forming as distributions shift (Alexander 2015). These range changes might lead to competitive exclusion or introgressive hybridization, which may eventually lead to the extinction of inferior competitors or genotypes (Parmesan 2006, Urban *et al.* 2012). Documenting such occurrence patterns is essential for understanding and anticipating species distributions in the context of climate change (Araújo and Luoto 2007, Urban *et al.* 2016).

Synchronous range dynamics have been observed in the two most common native felids in North America, the bobcat (*Lynx rufus*) and the Canada lynx (*Lynx canadensis*). The Canada lynx range has contracted by 40% compared to its historical extent in the 18th century (Laliberte and Ripple 2004). In contrast, the bobcat (*Lynx rufus*) seems to be reclaiming its historical range after a decline due to overharvest in the 20th century and expanding its range northward into lynx territory (de Vos 1964, Lavoie *et al.* 2009, Roberts and Crimmins 2010). At the turn of the 20th century, scientists noted how the ranges of these two felids seemed to be changing simultaneously (de Vos 1964, Hoving *et al.* 2003). The progression of bobcats into former lynx habitat could be a result of land clearing, since bobcats seem to prefer the more open habitat and young deciduous forests (de Vos 1964). However, there are some exceptions to this general trend. In British Columbia, Canada, the two species' ranges seem not to have changed since 1935 (Gooliaff and Hodges, 2018).

The potential for competition between bobcats and lynx has been debated (Aubry *et al.* 2000, Buskirk *et al.* 2000, Gooliaff and Hodges 2018, Gooliaff *et al.* 2018, Hoving *et al.* 2003, Newbury *et al.* 2018, Peers *et al.* 2013, Parker *et al.* 1983, Schwartz 2004, Scully *et al.* 2018). Some have reasoned that the potential for competition is high, because the species are closely related and morphologically similar, and use similar resources (Peers *et al.* 2013). In contrast, some authors have indicated that coexistence between bobcats and lynx also seems possible, because they have different dietary strategies and no demographic impact has ever been reported by one species on the other in an area of sympatry (Newbury *et al.* 2018). Bobcats are often described as habitat generalists that prey on a variety of species (Hansen 2007, Larivière and Walton 1997, McCord and Cardoza 1982), whereas lynx are snowshoe hare (*Lepus americanus*) specialists (Parker *et al.* 1983, Saunders 1963). In this time of unprecedented warming of the climate, if there is interspecific competition, lynx may be at a disadvantage since changing snow regimes may reduce the abundance of its main prey, the snowshoe hare (Krebs 2010).

Some studies have discussed interactions between the two species. Parker *et al.* (1983) reported that bobcats expanded into former lynx habitat in Cape Breton, Nova Scotia. However, there was no evidence of interaction between the species. Peers *et al.* (2013) conducted a broad-scale continental analysis and suggested that lynx and bobcats might compete for resources. In sympatry, lynx exploited a narrower range of environmental characteristics relating to climate (*e.g.* snow depth, minimum temperature of the coldest month) and elevation, whereas bobcats broadened their niche. In British Columbia, Canada, Gooliaff *et al.* (2018) found that bobcats were restricted to the south, whereas lynx were found in the interior. The two species did, however, overlap in the southern part of the province, but lynx were generally found at higher elevations than were bobcats. In another study in northern Washington, USA, Scully *et al.* (2018) found that lynx avoided camera sites where bobcats were present. In general, these studies provide some evidence of spatial avoidance from a continental to population scale between these closely related felids.

In many cases snow conditions have been suggested to be important limiting factors for bobcats, essentially limiting their progression into lynx territory (Hoving *et al.* 2003, Marston 1942, McCord 1974, Parker *et al.* 1983). For example, Parker *et al.* (1983) suggested that deep winter snow kept bobcats from moving into the Cape Breton highlands of Nova Scotia, Canada. Bobcats were, however, able to colonize and establish a breeding population on the lowlands of the island where winter snow is much shallower than the highlands immediately after the construction of a causeway to the mainland in 1955 (Matlack and Evans 1992, Parker and Smith 1983). Both species are similar in weight, but lynx have much larger feet and can support at least twice the weight compared to bobcats at the same snow density (Parker *et al.* 1983). Accordingly, lynx likely have a competitive advantage over bobcats in catching prey in deep snow conditions (Anderson and Lovallo 2003, Larivière and Walton 1997, Nowak 1999). Conversely, bobcats generally occupy areas in North America that have shallow or no snow (Nowak 1999).

There are few field studies of sympatric populations of bobcats and lynx and these studies have been limited to the contact zone in western North America (Gooliaff *et al.* 2018, Scully *et al.* 2018). Other than anecdotes by Parker *et al.* (1983) and broad scale analyses using genetics

(Koen et al.2014a) and occurrences from museum and harvest records (Peers *et al.* 2012, 2013), regional or finer scale field studies have not been undertaken elsewhere. In northern Ontario, Canada, the number of incidentally harvested bobcats has been increasing since the early 1990s, whereas the number of harvested lynx has been relatively stable since the mid-80s (Figure 6.1). Bobcats were first reported by trappers in northwestern Ontario at the beginning of the 20th century, while reports in the northeast near Sault Ste. Marie, Ontario began in the 1940s (de Vos 1964, Peterson and Downing 1952). After the early 1940s, the number of bobcats harvested increased steadily and bobcats were harvested farther north each year (de Vos 1964). From 1964 until present day, bobcats likely continued their progression into the province, based on summaries of annual fur harvest data (Figure 6.1). Conversely, even though the total number of harvested lynx has recently been stable, the range of the lynx has been contracting northwards (Koen *et al.* 2014b). The range contraction of lynx might be associated with the current bobcat range expansion. It seems that over the past several decades, bobcats have expanded into areas that were once occupied by lynx. It is unknown whether the incursion of bobcats is the cause of the lynx range contraction or whether bobcats have spread into habitat after it has already been vacated by lynx. In any case, these dynamic processes might provide additional insight into how these closely related species coexist in a contact zone.

We assessed home-range level occupancy of bobcats and Canada lynx on the north shore of Lake Huron in Ontario, Canada. We sought to determine to what degree the space and habitat use of these species overlap in an area of regional scale range sympatry. We hypothesized that if there was spatial segregation between the two species, then there would be a negative relationship between their occupancies. We also hypothesized that if there was habitat partitioning, then there would be measurable differences in land cover, prey, and snow conditions associated with the habitat used by each species.

Considering the geography of our study area within the northern range of the bobcat and its generalist nature, we predicted that bobcats occupy areas in the south that that are predominantly human altered (agricultural fields, pastures, urban areas, roads, etc.). Bobcats in these areas should be exposed to a higher diversity of prey species associated with anthropogenic environments, and shallower, more compacted snow. In contrast, given their habitat specialist nature, lynx should occupy forest stands with coniferous cover, low human disturbance, and a low diversity of prey species, but high snowshoe hare and red squirrel (*Tamiasciurus hudsonicus*) activity. Consequently, because of their respective habitat preferences and differing abilities to move through deep snow, we predicted that bobcat and lynx occupancy would have an inverse relationship throughout the study area. In general, we sought to record the current state of the spatial and habitat patterns in this area of dynamic range overlap to aid in evaluating causes of current and future range limits.

Materials and Methods

We used snowmobile surveys to collect track occurrences of bobcats and lynx in an area of range overlap located on the north shore of Lake Huron between Sault Ste. Marie and Sudbury, Ontario, Canada from 2016 to 2018, inclusive. Within an area of 32,832 km^2, we identified 41 survey routes and attempted to survey each one repeatedly from January until the end of March (Figure 6.2). While conducting these surveys, we estimated prey activity and snow depth and hardness. We also estimated the probability of occupancy of both species from independent occupancy models while accounting for detectability. We then compared the n-dimensional niche of each species and investigated the potential for habitat overlap. We tested for spatial segregation and niche overlap between bobcats and lynx.

Sampling extent and survey units

Since the 1970s, bobcats have been almost exclusively caught in traplines and townships found within the Algoma and Sudbury districts of Ontario, except for a recent increase in northwestern Ontario between 2011 and 2014 (Figure 6.1). To define the extent of our study area, we calculated the minimum convex polygon (MCP) of bobcat trapping records (2000 to 2005). We buffered the 75% MCP by 35 km to accommodate nearby traplines or townships. We then divided our study area into 513 hexagonal sampling units of 64 km^2. The area of these units is equivalent to the home range size of a female bobcat or lynx at the fringe of its geographic distribution (Squires *et al.* 2012, Fuller *et al.* 1985). Ideally, we wanted a maximum of 1 female bobcat per sampling unit, so that we could assume that occupancy of each sampling unit was spatially independent. The study area has also historically contained abundant lynx populations (Fig. 6.1).

Selecting surveying units

We attempted to sample all land use classes and their combinations. We first preselected sampling units using a clustering algorithm. We clustered each sampling unit based on their associated land cover composition. We used the Ontario Forest Resource Inventory (OMNRF 2015) maps to categorize each forest stand by Provincial Forest Type and seral stage. Additional areas that were not forest stands were classified as agriculture, water, wetland, and a disturbed class that included developed areas. We then extracted the proportion of each class within each hexagon and clustered these data using Affinity Propagation (Frey and Dueck 2007). The sampling units clustered into 33 distinct groups characterized by different compositions of land cover. The algorithm produced an exemplar for each group that was the most representative unit of the group and was selected to be surveyed. In cases where the exemplar could not be surveyed due to accessibility, we instead attempted to survey the nearest unit from the same group.

Snowmobile survey routes

We surveyed 41 different routes over 3 winters from 2016 to 2018. In general, we attempted to map a snowmobile route to and through each selected survey unit with aerial photos, topographic maps, Google maps, and other geographic resources. After at least 48 hours but preferably 72 hours following a track-obliterating snowfall event, an observer followed the mapped route through each survey unit on a snowmobile at 20 km/hr. Due to access and time constraints, the average distance surveyed on each route was 9.09 km and the length of these routes ranged from 7 to 11.6 km. However, Squires *et al.* (2012) found that after 7 km of searching the probability of detection asymptotes. Only tracks found within a visible distance of the survey route were considered (~5 meters on either side of the observer).

Only 35 of these routes were used in the subsequent analysis (Figure 6.2), because for 6 transects, snow data was not collected, the route was only surveyed once, the route was never surveyed during good tracking conditions, or we could not assume spatial independence from other routes. For instance, we removed one survey route that ended up on the periphery of another sampling unit. Also, we removed a route that clustered our sampling in one location in our study area. The 35 routes were surveyed between 2 and 7 times over 3 years, and on average each route was surveyed 4.43 times to get an estimate of detectability.

Felid tracks

We recorded the number of times a set of bobcat or lynx tracks intersected the survey route. We recorded the location of each set of tracks on a GPS unit and noted descriptors of the quality of the track and the confidence of the identification. When a felid track was encountered, the track was also photographed and measured for documentation purposes. In addition, we followed tracks of uncertain identification to confirm species identity. In general, bobcat and lynx tracks in the study area were easy to discriminate because of differences in foot size and furred footpads (Elbroch and McFarland 2019).

Potential prey and carrion

There is no information on the diet of the bobcats in Ontario, but bobcats from our study area are part of a subspecies that includes the northwestern Great Lakes region (Reding *et al.* 2012). Studies from Minnesota and Wisconsin have reported that cervids and lagomorphs are the main prey for bobcats in this region and can on average make up 40.2 and 31.3% of the diet (Gilbert 2003, Rollings 1945). In addition, North American porcupine (*Erethizon dorsatum*), and smaller mammals and birds can make up to 12.3, 6.4 and 1.6% of the diet (Rollings 1945).

The nearest study of winter lynx diet, 500 km east in Minnesota, found that snowshoe hare (*Lepus americanus*) made up 92% of predation events (Hanson and Moen 2015). However, Roth *et al.* (2007) indicated that snowshoe hare may represent only 63% and 68% of lynx diets in Minnesota and Ontario. This suggests that although it is a specialist on snowshoe hare, the lynx might switch to alternative prey species when required (Roth *et al.* 2007). As an alternative to hares, lynx might prey on red squirrels, spruce or ruffed grouse (*Falcipennis canadensis* and *Bonasa umbellus*, respectively) and small mammals (Aubry *et al.* 2000, Hodges 2000). In the southern boreal forest, small mammals other than squirrels only make up 3-8%, and small birds 1-7%, of the diet of Canada lynx (Aubry *et al.* 2000).

Moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) carrion may be an important food source for bobcats (DeVault *et al.* 2003, Fritts and Sealander 1978, Litvaitis *et al.* 1986, Parker *et al.* 1983, Petraborg and Gunvalson 1962, Platt *et al.* 2010, Svoboda *et al.* 2013, Svoboda *et al.* 2019) and lynx (Brand *et al.* 1976, Nellis and Keith 1968, Saunders 1963).

We recorded track activity of both main and alternative prey species and potential carrion that both species would encounter in our study area. We recorded occurrences of North American beaver (*Castor canadensis*), eastern gray (*Sciurus carolinensis*) or American red squirrel, spruce or ruffed grouse, moose, North American porcupine, raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), snowshoe hare, wild turkey (*Meleagris gallopavo*), and white-tailed deer. We did not account for small rodents and passerines due to our use of snow tracking as a sampling method, which is ineffective for assessing the abundance of these groups.

Due to time constraints, we stopped counting tracks for a given species after 100 tracks were reached on each transect. To account for this data censoring, we divided these censored values by the survey route length and multiplied this value (tracks per kilometer) by the length of the shortest survey route which was censored. To account for the different survey lengths of each route and track accumulation over time, we divided these values by the survey length and then divided by the number of days since the last snowfall. Therefore, these values were the rate of track accumulation of each species per kilometer per day since the last snowfall.

Statistical modelling

The observation of tracks on survey routes may be influenced by detectability. Under-detecting occupancy could be caused by animals not yet having moved through the area, tracks missed because of poor conditions, or tracks missed because of observer error. Therefore, when investigating influences on occupancy of an area it is suggested to account for detectability, since it may influence the parameter estimation of habitat predictors (MacKenzie *et al.* 2006). We modelled both bobcat and lynx occupancy using a single-season occupancy model based on a zero-inflated binomial distribution; covariates were modelled using a logit link (MacKenzie *et al.* 2006, Royle and Dorazio 2008). The predictors of these occupancy models were separated into 2 classes, observation-level and site-level covariates. Observation-level covariates may vary between sampling occasions (snow conditions, temperature, etc.), whereas site-level covariates are characteristics of a sampling location that remain somewhat constant (land use, land cover, prey density, etc.).

Observation-level covariates

In our analysis, the observation-level covariates described the general meteorological conditions during which the snowmobile surveys were undertaken and the quality of the tracking conditions. We accounted for tracking conditions using the number of days since the last snowfall. We also thought that the minimum temperature of the previous night would be a good indicator of whether bobcats or lynx would be active, since we noticed while we were live trapping and tracking these species with GPS collars that they were less active during nights that were below -20 C°. We also thought that the different lengths of the survey routes might influence detectability. We did not account for the year of the survey as an observation-level covariate, because this would have suggested that there was detectability bias between years. We consider this unlikely, because the same observer surveyed for snow tracks during the entire study. Also, the addition of a time index such as year in our occupancy model would have served as a surrogate for observation-level covariates, but the post-hoc interpretation of this time index would have been complicated, because it is generally uninformative and not biologically relevant (*e.g.*, Howe *et al.* 2013).

Site-level covariates

The site-level covariates included the potential habitat characteristics that bobcats and lynx avoided or were associated with within areas where they occurred. We accounted for 3 types of site-level covariates related to prey activity, snow conditions, and land cover. We generated two different types of prey indices. First, we estimated abundance of snow tracks of different prey species or species groups. We included the average track accumulation of prey species that were found on the survey route, but we only kept prey or carrion species that had an average track accumulation greater than 1 track per 10 kilometers in a day. Although we tracked the abundance of all potential prey we could observe using these methods, for our occupancy analysis, we focused on prey types that we considered particularly important for bobcats and lynx: hare, deer, grouse, and squirrel. As a second type of prey index, we estimated prey richness by counting the number of different prey or carrion species found on each route over the 3 winters (including rare species). However, we had to remove the effect of sampling effort for the richness measure, which in this case was the total distance surveyed on each survey route. We fit the total number of kilometers surveyed on each route to the number of prey species found using ordinary least squares regression. We then predicted the number of prey species that would be found on a 7 km route and added the residuals of each survey route to this value.

We accounted for the average snow conditions measured during the last 2 winters of the study (2017 and 2018) by calculating the average snow depth and snow hardness of each route over these 2 years. During each sampling occasion we measured snow depth and hardness 3 times at points evenly distributed across the survey route. Snow depth was measured with a metal meter stick and visually verified by digging away snow if necessary. Snow hardness was the depth that a 150 g plastic ball fell through the snow when dropped from a height of 1 meter above the surface of the snow. Consequently, a small value indicated compacted snow and a large value indicated soft snow.

We included the proportion of different land cover types found within a 1 km buffer of the survey route. Land cover covariates are the proportion of land occupied by anthropogenic disturbances (agricultural and rangeland, roads, highways, railways, urban areas, mines, etc.), wetlands (wetlands, lakes, and rivers), and the proportion of land occupied by coniferous, deciduous, and mixed forest, and their associated seral stage (immature or mature forest).

Occupancy analysis

We gathered many habitat predictors that were related to aspects of the niche of bobcats and lynx that have been investigated in the past. Unfortunately, many of these predictors were collinear, which may cause unstable parameter estimates, inflated standard error, and potentially biased inference (Dormann *et al.* 2013). Consequently, we used principal component analysis to create orthogonal latent predictors that represented habitat gradients found across our survey routes. We first selected significant principal components using the Auer-Gervini method (Auer and Gervini 2008) with the R package “PCDimension” (Coombes and Wang 2018). We then selected latent predictors that we could easily relate to measured habitat characteristic. We used a Pearson correlation coefficient to identify the habitat characteristics responsible for the major variation of each principal component or latent predictor. We discarded latent predictors that did not have an absolute Pearson correlation above 0.5 against any habitat descriptor. We further limited these latent predictors to those that described more than one habitat condition. This left us with a reduced set of latent predictors that described several major habitat gradients that might explain bobcat and lynx occupancy across our survey routes.

We chose the models with the lowest AICc. If there were any models within 2 ΔAICc from the top model we used model averaging. We then further investigated the relationship between probability of occupancy (Ψ) and detection (ρ) for each species and habitat gradients. Next, we predicted the probability of detection of both species during each survey to calculate the average probability of detection, and we also predicted the probability of detection of the two species over all 3 observation-level covariates. We predicted the probability of occupancy over the range of each predictor found in the top models to investigate their importance. We also predicted the probability of occupancy of each species over our study area to investigate the spatial relationship and potential habitat overlap between bobcats and lynx. When investigating the importance of a covariate over Ψ and ρ, we fixed other covariates to the median value found on our survey routes. We fit all occupancy models with the package "unmarked" (Fiske and Chandler 2015) in R version 3.5.1 (r-project.org). We used the function "occu" within the unmarked package.

Results

Of the 35 routes used in the analysis, lynx tracks were found on 16 routes, bobcat tracks were found on 11 routes, and neither species was found on 8 routes. We never found both species on the same survey route. Of the 155 surveys, lynx tracks were found on 39 surveys and bobcat tracks were found on 19 surveys. Lynx track activity ranged from 0 to 4 crossings per survey and bobcat ranged from 0 to 3 crossings. Bobcats were generally found near the shores of Lake Huron whereas lynx were found in areas slightly farther north or inland (Figure 6.2).

The survey routes were dominated by deciduous mature forest (Figure S1). However, lynx occupied areas with a higher average proportion of coniferous forest and bobcats were on average more frequently found in areas with a higher proportion of anthropogenic disturbance and near wet areas (wetlands, rivers, or lakes). On the survey routes, we found track evidence of beaver, squirrel, grouse, moose, porcupine, raccoon, skunk, hare, turkey, and deer (Figure S2). Bobcats and lynx occupied areas with similar beaver, squirrel, grouse, moose, and snowshoe hare track activity. However, sites occupied by bobcats had skunk, porcupine, and turkey, whereas sites occupied by lynx did not. Also, routes with bobcats had on average higher track activity of white-tailed deer and raccoon. In addition, areas with bobcat activity had higher average prey richness compared to areas where lynx tracks were found (Figure S3). Finally, the snow conditions of survey routes where lynx tracks were found were similar to those of routes on which bobcat tracks were found (Figure S4).

Principal Component Analysis

We performed a principal component analysis on 14 of 20 of the habitat variables (Figure S5). We only included snowshoe hare, squirrel, deer, and grouse as prey in the analysis, since track accumulation was generally higher for these prey items across the study area, and we suspected that these species were particularly important resources for bobcats and lynx. The Auer-Gervini method indicated that up to 6 principal components were likely signals and not noise in the data. However we further investigated and found that only 4 principal components best described these 14 habitat predictors and the remaining axes were difficult to interpret, because we could not easily link them back to the habitat variables (*i.e.*, there was a low correlation) or only a single habitat characteristic dominated the loadings of the principal component (*e.g.*, components 5-6). The 4 principal components that we included each explained over 9% of the variance and all 4 combined explained 69.3% of the total of the habitat predictors. These latent predictors described 4 orthogonal habitat gradients found across our 35 survey routes that we used as predictors in our subsequent bobcat and lynx occupancy models (Table 6.1).

Occupancy models

Models with more than 3 site-level covariates did not converge. This was most likely due to a lack of degrees of freedom on the site-level of the hierarchical model. Therefore, we only investigated up to 3 covariate combinations and consequently 15 models for both bobcat and lynx.

The average probability of detection for lynx was 1.59 times higher than for bobcats in the study area over all 3 winters (0.29/0.46; Figure S6). After we averaged the top models, we found very different effects of observation-level covariates on detection (Figure S7). We found that the number of days since the last snowfall did not seem to influence bobcat detectability but had a positive effect on lynx detectability. The temperature of the previous night had no effect on detectability of either species. Finally, the length of the survey route was positively associated with the detectability of bobcats but did not influence lynx detectability.

For both species, we found that the top models contained both principal components 2 and 4 (Table 6.1 and Figure S8). For bobcats, we found that a single top model had a ΔAICc of > 2 higher than the remaining models, so we did not have to perform any model averaging. The top model for lynx was the same, but an additional model was within 2 ΔAICc units of this model. This model contained the solitary effect of principal component 2. We first averaged the lynx models and then we investigated the effect of principal components 2 and 4 on the probability of detection and occupancy of both species.

Principal component 2 represented a gradient of snowshoe hare, grouse, squirrel, prey richness, anthropogenic disturbances, and coniferous forest (Table 6.1). The habitat on one end of the gradient had a mix of several different land cover types with several options of prey and high prey activity, and the other end of the gradient the land cover was dominated by coniferous forest with a low number of prey options and low prey activity. The occupancy probability for bobcats and for lynx increased at opposing ends of this gradient. Bobcat occupancy increased with habitat heterogeneity and lynx occupancy increased with habitat homogeneity (Figure 6.3a). More specifically, human-disturbed areas with high activity of snowshoe hare, grouse, and squirrel, high prey richness, and a low proportion of coniferous forest were areas where bobcat probability of occupancy was high and lynx probability of occupancy was low. Conversely, homogenous areas less disturbed by humans with low activity of snowshoe hare, grouse, and squirrel, low prey richness, and a high proportion of coniferous forest were areas where bobcat probability of occupancy was low and lynx probability of occupancy was high.

Principal component 4 represented a gradient of grouse, deer, prey richness, snow depth, and proportion of mixed forest. On this gradient, deer activity increased with prey richness but decreased with increasing grouse activity, snow depth, and mixed forest. Bobcat probability of occupancy increased towards higher values of this predictor, but the effect of this gradient seemed negligible for lynx (Figure 6.3b). The probability of occupancy of bobcats was higher in areas with high deer activity, high prey richness, low grouse activity, shallow snow, and a low proportion of mixed forest.

Occupancy and Overlap

We predicted the probability of occupancy of both species and found that bobcats occupied areas closer to the shore of Lake Huron whereas lynx occupied areas away from the shores (Figure 6.2). There was a discrepancy in this pattern near the shore just to the east of the middle of the study area, where bobcat occupancy was low, and lynx was much higher. However, bobcat occupancy was higher on the shore eastward. Finally, we found that as bobcat occupancy increased, lynx occupancy decreased in our study area ($R^2 = 0.84$; Figure 6.4).

Discussion

We hypothesized that bobcats and lynx are spatially segregated on the north shore of Lake Huron. We found support for this hypothesis because both species were never found on the same survey route over 3 winters, and consequently, they appeared to be completely segregated in our study area (Figure 6.2). There was also a negative relationship between their probability of occupancy (Figure 6.4). We also found support for our hypothesis of habitat partitioning by land cover types, prey, and snow conditions (Figure 6.3). Our findings agree with Farrell *et al.* (2018), where bobcats had an affinity for heterogenous areas that were avoided by lynx. We found that these two felid species coexist in this area of broad-scale sympatry either by avoiding each other or by exploiting different niches at the population level. Unfortunately, both processes could have resulted in the observed patterns, therefore we were not ultimately able to determine their cause. Overall, we found no evidence for competition, although we cannot discriminate between competition and habitat selection as processes leading to the complete spatial segregation that we observed between these species. However, given that bobcats are expanding their range northwards, a lack of spatial overlap suggests that bobcats are moving into suitable habitats, which tend to be sites unoccupied by lynx.

Generalist and specialist

We found that bobcats and lynx probability of occupancy increased at opposing ends of a habitat gradient (Figure 6.3a). Heterogeneous, anthropogenically disturbed landscapes were at one end of this spectrum and occupied by bobcats. A more homogenous natural area dominated by coniferous forest stands was at the other end, occupied by lynx. We also found that bobcat probability of occupancy increased in areas of high prey richness and lynx occupancy increased in areas of low prey richness (Figure 6.3). These land cover and prey patterns matched the reputation of bobcats as a habitat generalist and lynx as a specialist on snowshoe hares (Anderson and Lovallo 2003, Peers *et al.* 2012).

Snow conditions

We hypothesized that areas where bobcats occur have, on average, shallower and more compacted snow compared to areas occupied by lynx. We found that survey routes where bobcat tracks were found had on average similar snow depth and hardness compared to survey routes where lynx tracks were found (Figure S4). However, we also found that bobcat occupancy increased with decreasing snow depth and this suggests that snow depth may be a limiting factor for bobcat expansion in our study area (Figure 6.3b). McCord (1974) suggested that bobcats have a difficult time traveling through the snow with a sinking depth exceeding 15 cm. We did not measure the sinking depth of individual cats, but we observed no differences in snow hardness between routes where bobcats and lynx were observed. Future studies should measure the individual sinking depth in relation to snow depth and snow hardness, within a reasonable timeframe from when the track was left as snow hardness is quite variable throughout the day (Figure S9). The daily movements of individuals could be influenced by this relationship, but not the occupancy of a bobcat in an area. In addition, our study area is within the vicinity of both Lake Superior and Lake Huron, and this area is frequently hit by lake-effect snowfall or snow squalls with over 15 cm of snow accumulation in a single day. However, these events are becoming less common due to the warming climate and the long-term trend will most likely favor bobcats (Baijnath-Rodino and Duguay 2018).

Range expansion and contraction

We expect that any decrease in coniferous forest cover in our study area will likely favor bobcat expansion. Like Farrell *et al.* (2018), our results suggest that bobcat expansion may have been mediated by human disturbances such as land clearing and forestry. Future expansion could be amplified by: (1) increasing disturbance such as roads, rail lines, urban areas, rangeland, agricultural land, etc.; (2) reducing coniferous forest cover, which is already undergoing a changeover to broadleaf species due to climate warming (Fisichelli *et al.* 2014); (3) changing snow conditions; or (4) increasing prey richness and prey activity. Increased prey activity (mostly snowshoe hare and squirrels) is likely related to a higher proportion of mast producing trees and shrubs, and also edge habitat, which has a higher density and diversity of food types (Mowat and Slough 2003, Theberge and Wedeles 1989). Edge habitat and mast producing tree and shrubs are more common on the shores of Lake Huron, because of the higher proportion of disturbances and the diverse land cover and land use types. Increased prey richness in our study area was due to species such as turkeys, raccoons, skunks, and deer, which are more likely to occur near human-disturbed areas and have been also expanding northwards in recent decades. Many of the environmental changes that increase heterogeneity and thereby facilitate the northwards expansion of bobcats will also likely contribute to continued range contraction of the Canada lynx range.

Interspecific competition

Considering the short duration of our study, we cannot answer with certainty whether these species are competing in this region. However, we observed no evidence of competition over the 3 years we studied these animals on the shores of Lake Huron. We know that the number of bobcats has increased since the early 1990s and the lynx range has been contracting northward. If there was contemporary competition leading to the lynx range contraction, we might have expected to find bobcats had spread into at least some areas where lynx also occurred and active competition processes underway. However, we found complete spatial segregation, such that no survey routes ever had evidence of both species.

In this study area, it previously seemed that the bobcat and lynx range fronts were moving northwards (de Vos 1964), and this pattern has not yet been documented in recent peer-reviewed publications. One main reason is that there are no recent studies investigating bobcats at their northern range limit in central Canada (de Vos 1964) and there are few studies that have investigated lynx in this area of range overlap (Koen *et al.* 2014b). We currently have only these few publications and aggregate level data from trapping records on which to base any inference (Figure 6.1). However, trappers, conservation officers, and government researchers have corroborated the pattern of lynx range contraction and bobcat range expansion. Although, like Gooliaff and Hodges (2018), it would be of great interest to investigate the trapping records of these species in our study area and determine whether there are any spatiotemporal patterns that might indicate whether the presence of bobcats negatively affects the probability of occupancy of lynx since its expansion in the late 1940s. Regardless, due to the northward movement of the range fronts of these species that is coincident with the observed spatial and habitat segregation, we consider it unlikely that interspecific competition is taking place. In contrast, Peers *et al.* (2013) found evidence of broad-scale niche displacement that suggested competition. Competition may be taking place at a coarser scale, but at a population level on the north shore of Lake Huron, we found no evidence of competition between these congeneric species.

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Authors' contributions

RRM and JB conceived the ideas and designed methodology; RRM and SJM collected the data; RRM analyzed the data; RRM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Tables

Table 6.1. Correlation matrix between all 4 major principal components and habitat characteristics for snowmobile routes surveyed for bobcat and lynx snow tracks during January-March from 2016 to 2018 in Ontario, Canada. The first 4 PCs explained 69.3% of the variance. Values shaded in grey indicate covariates that are major contributors to each principal component.

Covariates	**PC1**	**PC2**	**PC3**	**PC4**
Anthropogenic Disturbance	0.00	-0.65	-0.10	0.15
Coniferous Forest	-0.54	0.62	-0.05	0.28
Deciduous Forest	0.82	-0.29	0.19	-0.04
Deer	0.01	-0.26	0.51	0.56
Grouse	-0.18	-0.63	-0.01	-0.45
Immature Forest	-0.75	0.34	0.35	0.10
Mature Forest	0.87	-0.02	-0.16	-0.11
Mixed Forest	-0.70	0.09	0.00	-0.48
Richness	0.00	-0.63	-0.28	0.56
Snow Depth	0.65	0.25	0.27	-0.38
Snow Hardness	0.47	0.36	0.47	0.12
Snowshoe hare	-0.45	-0.56	0.46	-0.17
Squirrel	-0.18	-0.52	0.65	-0.09
Wetland	-0.27	-0.41	-0.50	-0.09

Figures

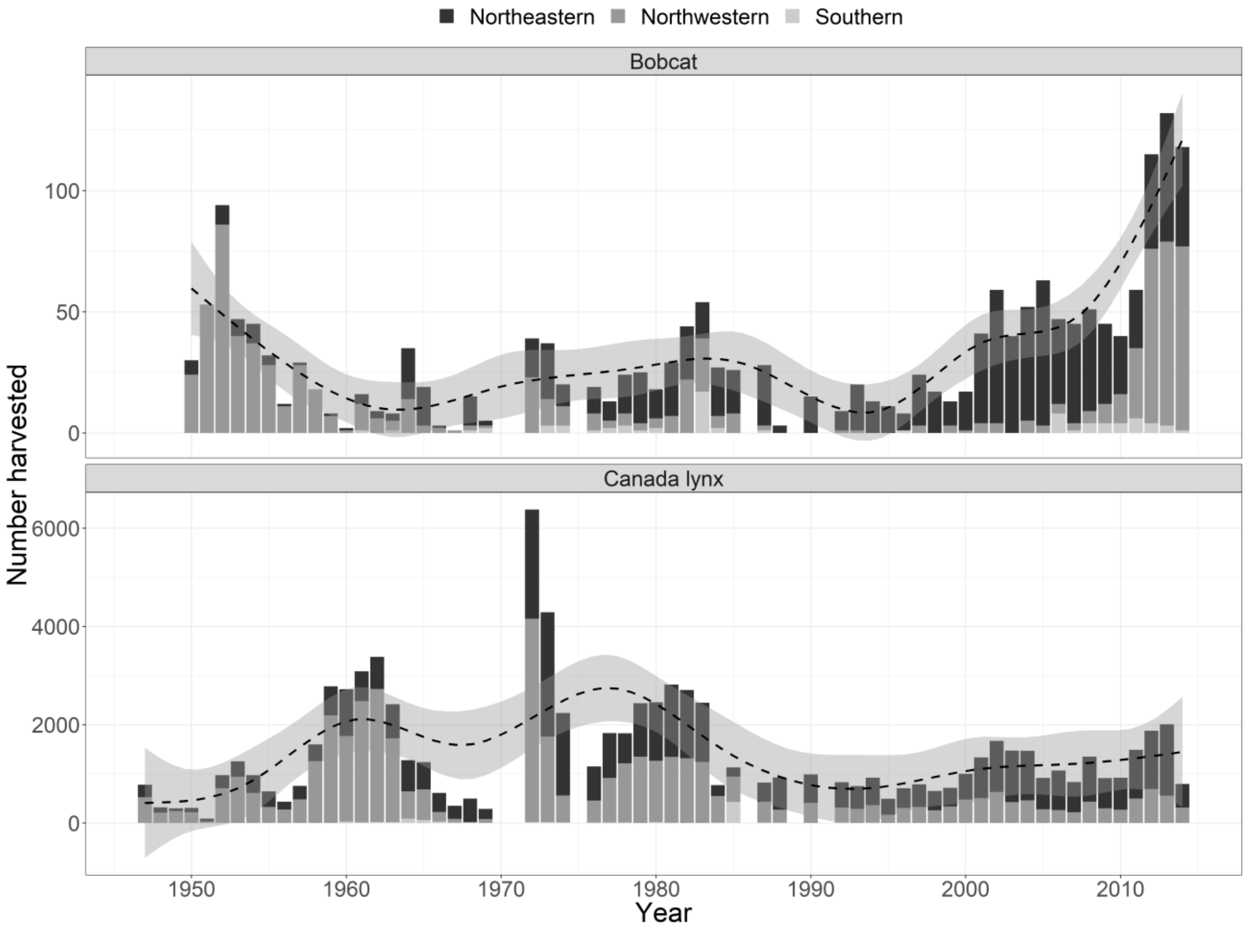

Figure 6.1. The number of bobcat and lynx harvested in Ontario, Canada between 1947 and 2014. Snow tracking surveys were conducted in eastern Ontario between Sault Ste. Marie and Sudbury, Ontario, Canada. The 'southern' area is the summation of central, eastern and southwestern Ontario where bobcat and lynx are seldom harvested. Harvest records were supplied by the Ontario Ministry of Natural Resources and Forestry. The dashed line is the line of best fit of the total number of individuals harvested over time, and the shaded band is the standard error. The generalized additive models were fit with the 'gam' package (Hastie and Hastie 2018).

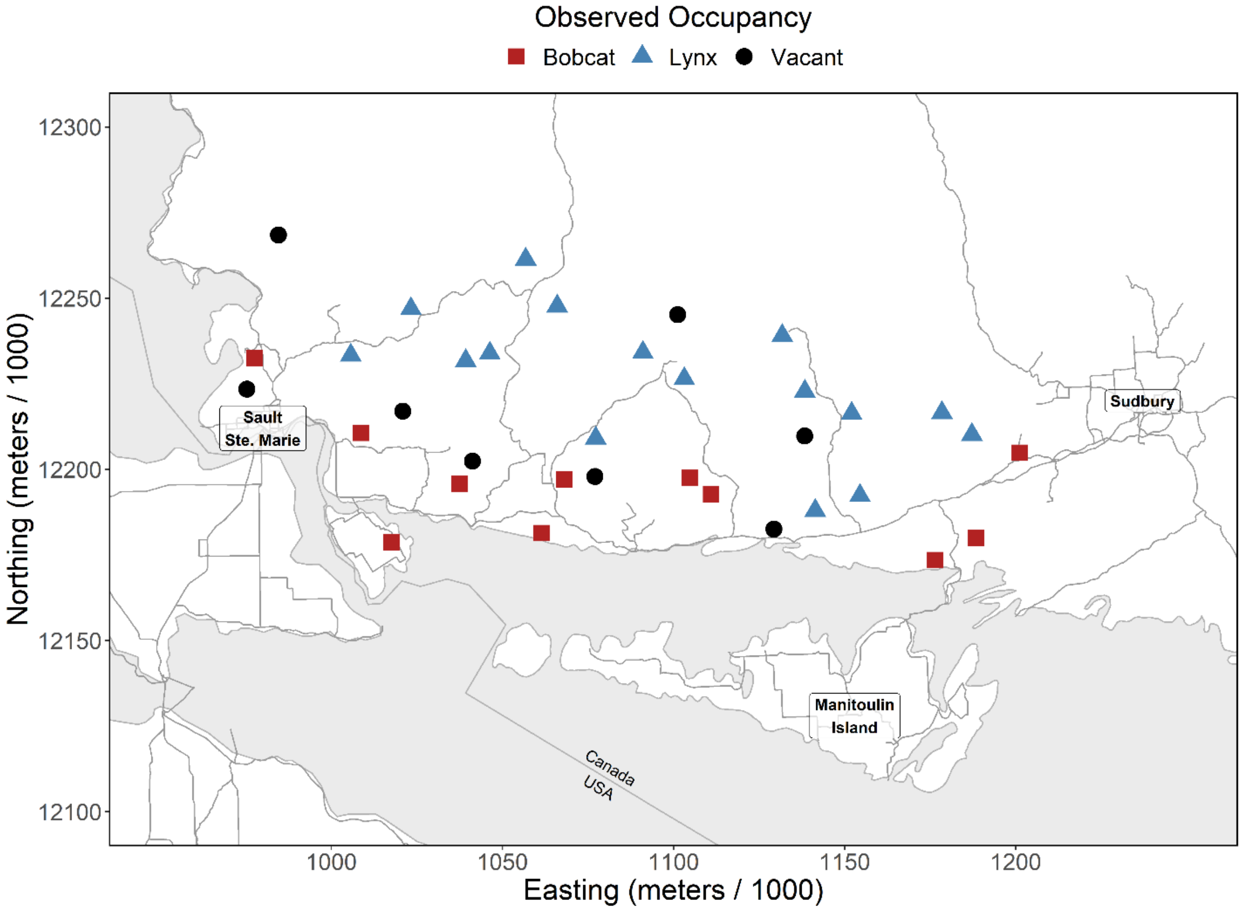

Figure 6.2. The area surveyed for bobcat and lynx snow tracks during January-March from 2016 to 2018 in Ontario, Canada. Shapes indicate the observed occupancy of each species on snowmobile survey routes. We never found both species on the same survey route. Projection is NAD83/Ontario Lambert. The administrative boundaries were sourced from GADM, the Database of Global Administrative Areas (GADM 2018) and are freely available to create maps for academic publishing. The road layer is in the public domain and is freely available from Natural Earth (naturalearthdata.com) without any restrictions. Map created in R version 3.5.1 (r-project.org) with the package "ggplot2" (Wickham 2016).

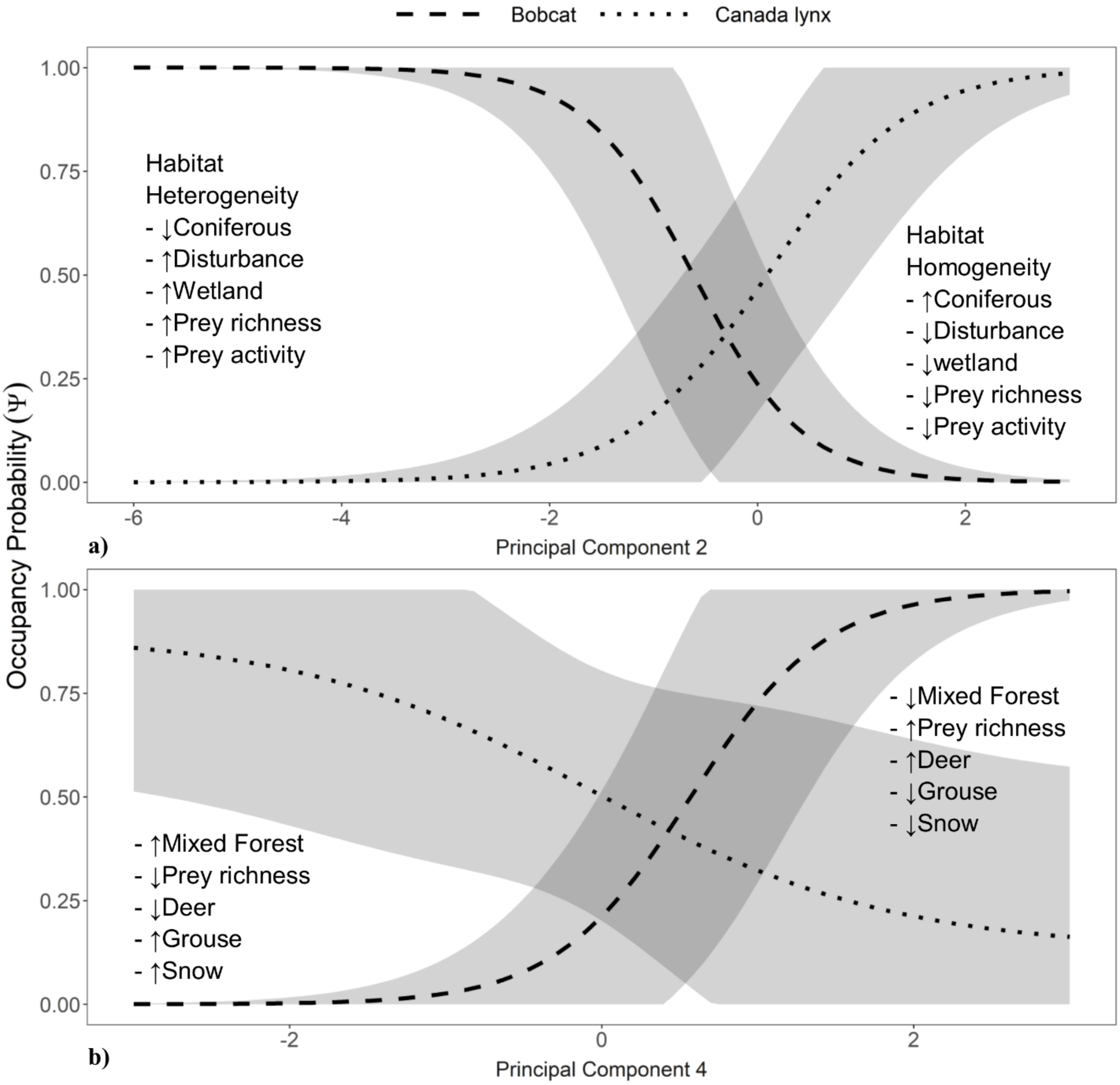

Figure 6.3. a) Predicted probability of occupancy of bobcat and lynx in accordance with PC2. A heterogeneous to homogeneous land cover and prey gradient. The vertical line indicates an area of potential habitat overlap between the two species. The shaded areas are the 95% confidence interval (Ψ ± se). b) Predicted probability of occupancy of bobcat and lynx in accordance with PC4.

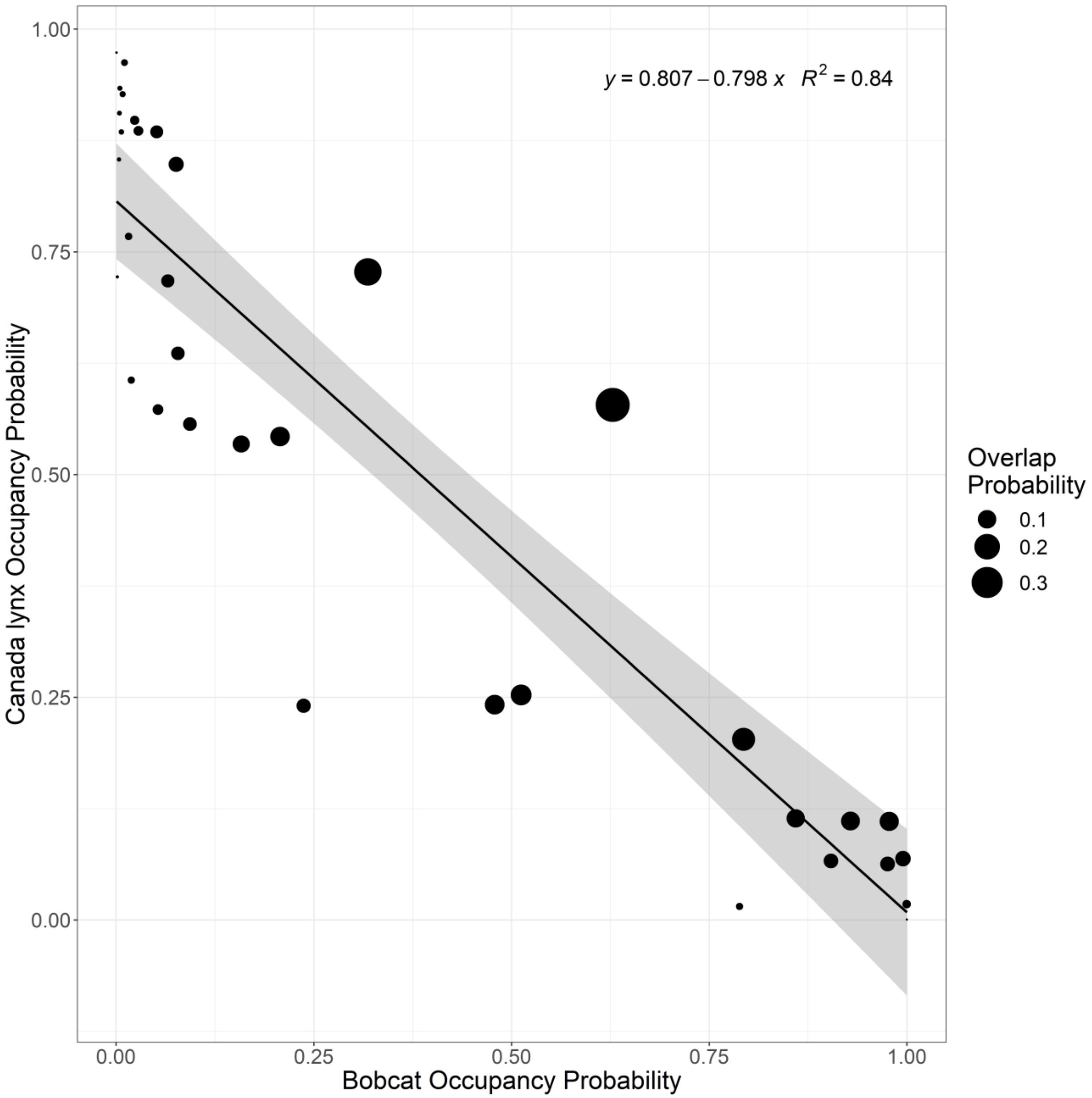

Figure 6.4. Predicted probability of occupancy of bobcat vs lynx. Overlap probability is the multiplication of the predicted probability of occupancy of bobcat and lynx (Ψbobcat x Ψlynx). The size of each point indicates the probability of overlap between both species.

Supplemental Figures

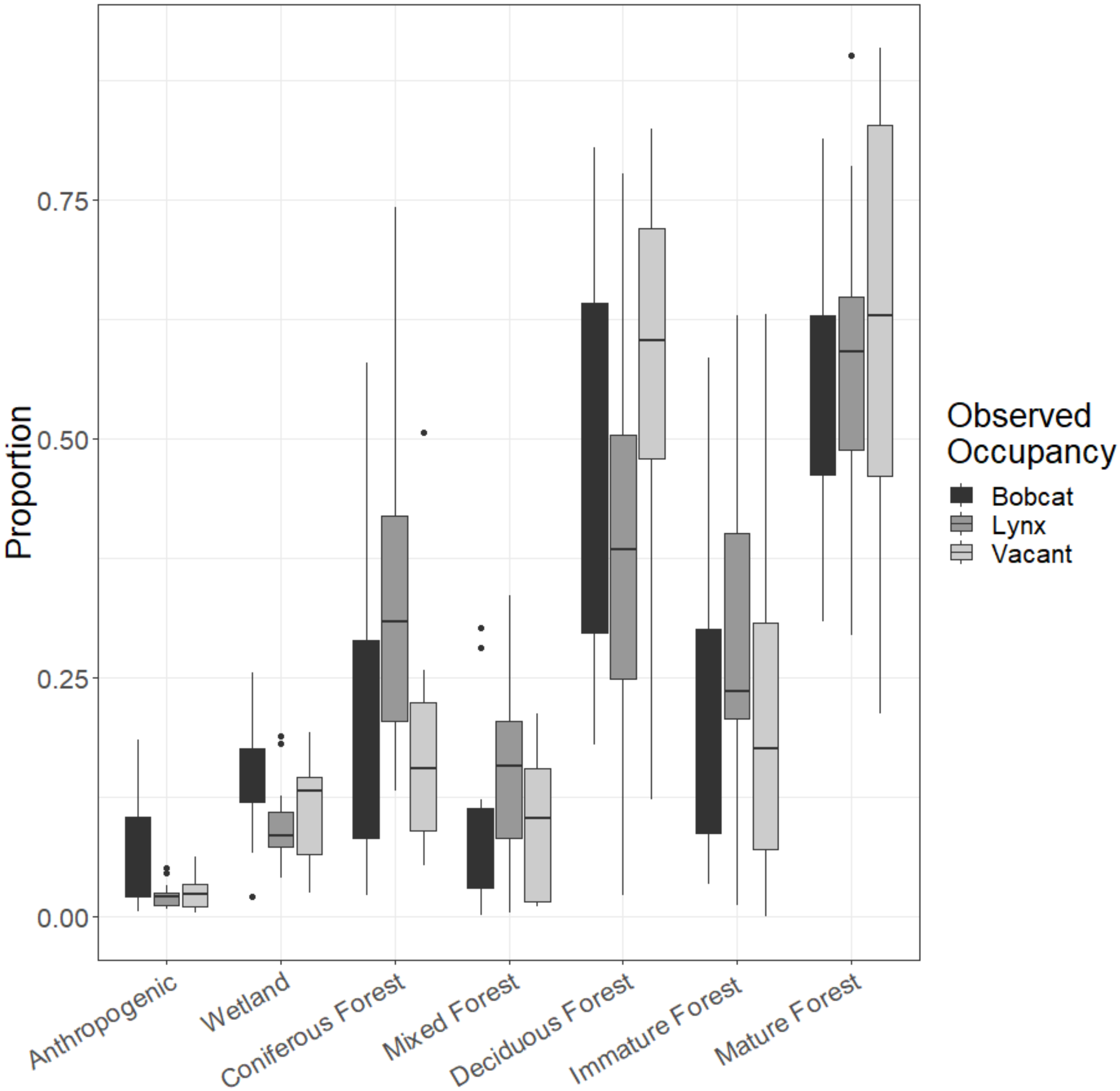

Figure S1. The proportion of land cover/use types of snowmobile routes surveyed for bobcat and lynx snow tracks from 2016 to 2018 during the months of January to March in Ontario, Canada. We applied a 1 km buffer to each route to calculate the proportion of each land cover/use type. The study area was predominately covered by mature deciduous stands.

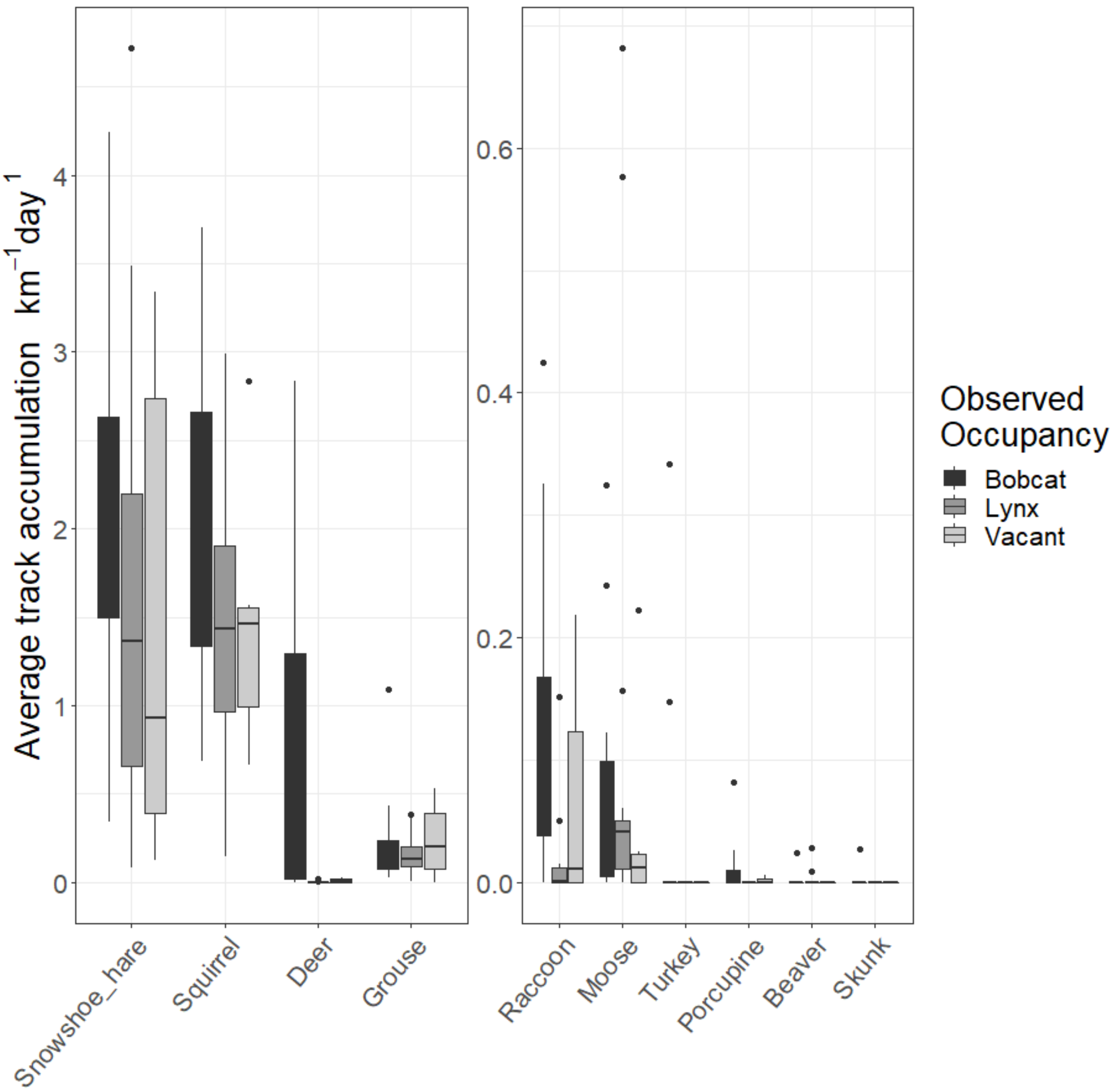

Figure S2. Average track activity of prey species found on snowmobile routes surveyed for bobcat and lynx snow tracks from 2016 to 2018 during the months of January to March in Ontario, Canada. We accounted for the density of tracks by dividing by the snowmobile route length and we also accounted for track accumulation by dividing by the number of days since the last snowfall. Turkey, porcupine, and skunk were never observed on routes where lynx occurred.

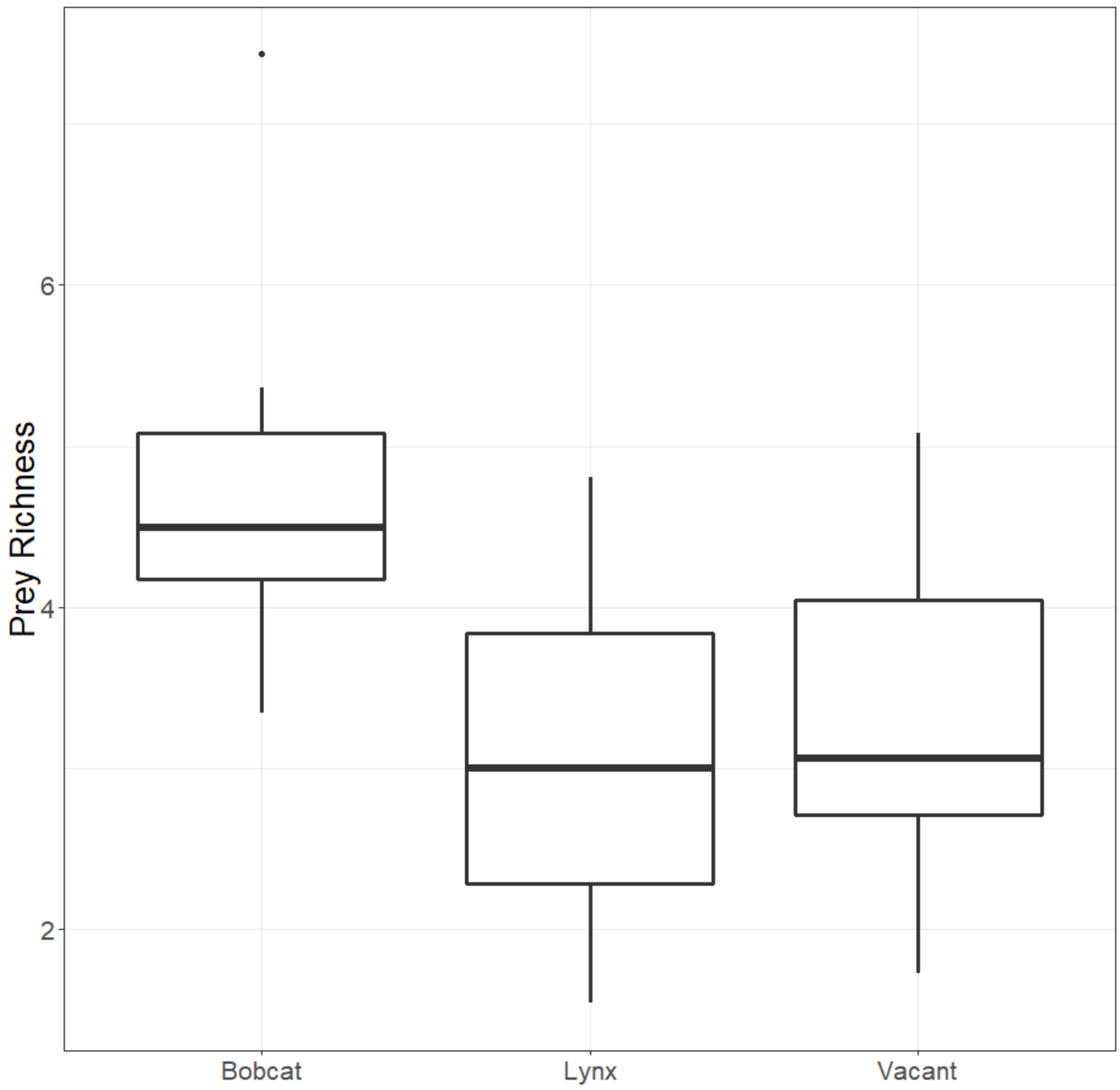

Figure S3. Prey richness of snowmobile routes surveyed for bobcat and lynx snow tracks from 2016 to 2018 during the months of January to March in Ontario, Canada. To account for the varying effort of each survey route, we used a linear model to remove the effort and added the residuals to the predicted prey richness of a 7 km long survey route.

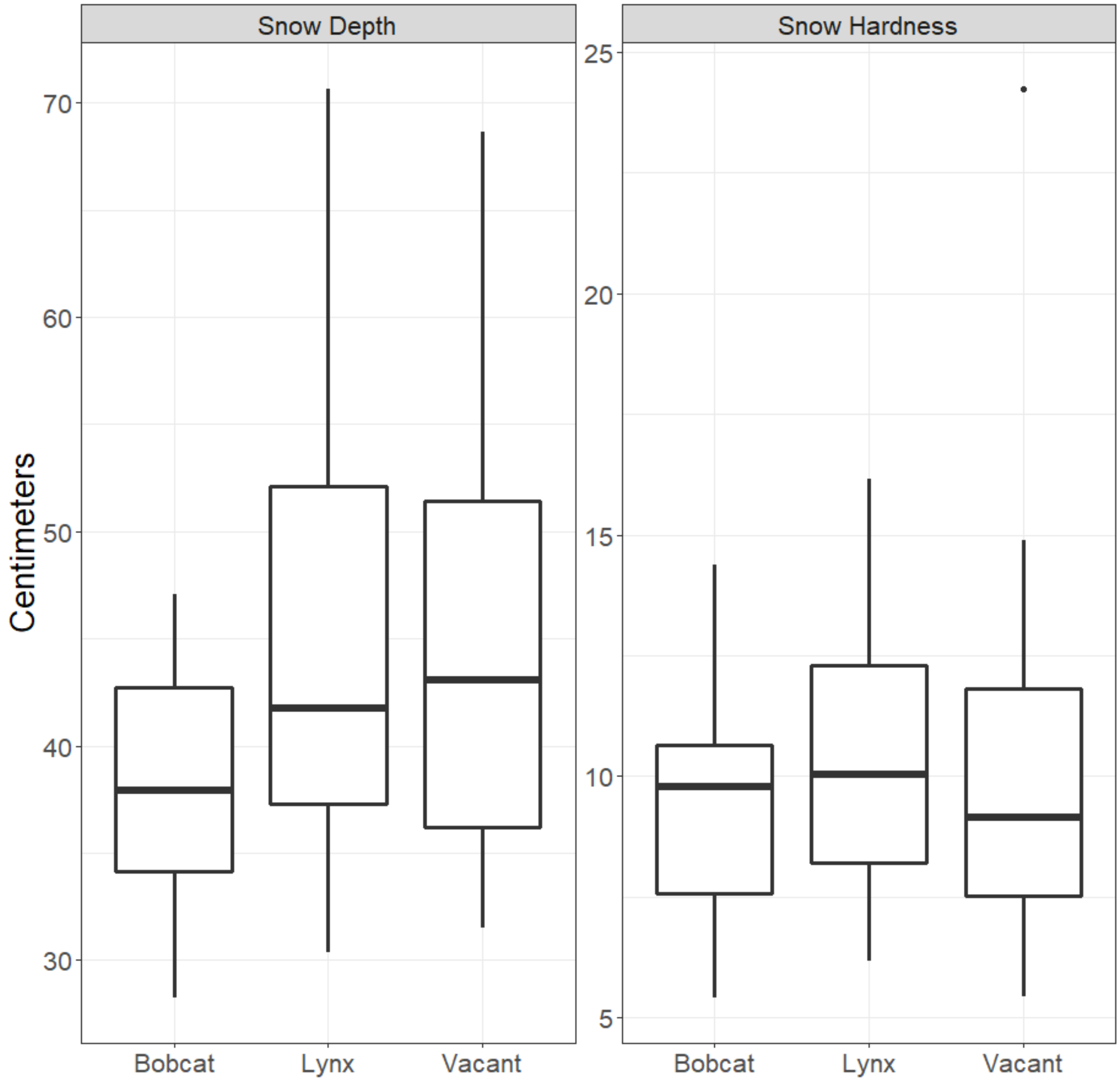

Figure S4. Average snow conditions of snowmobile routes surveyed for bobcat and lynx snow tracks from 2016 to 2018 during the months of January to March in Ontario, Canada. Snow hardness is the depth that a 150 g ball falls through the snow after it is dropped from a height of 1 meter from the surface of the snow.

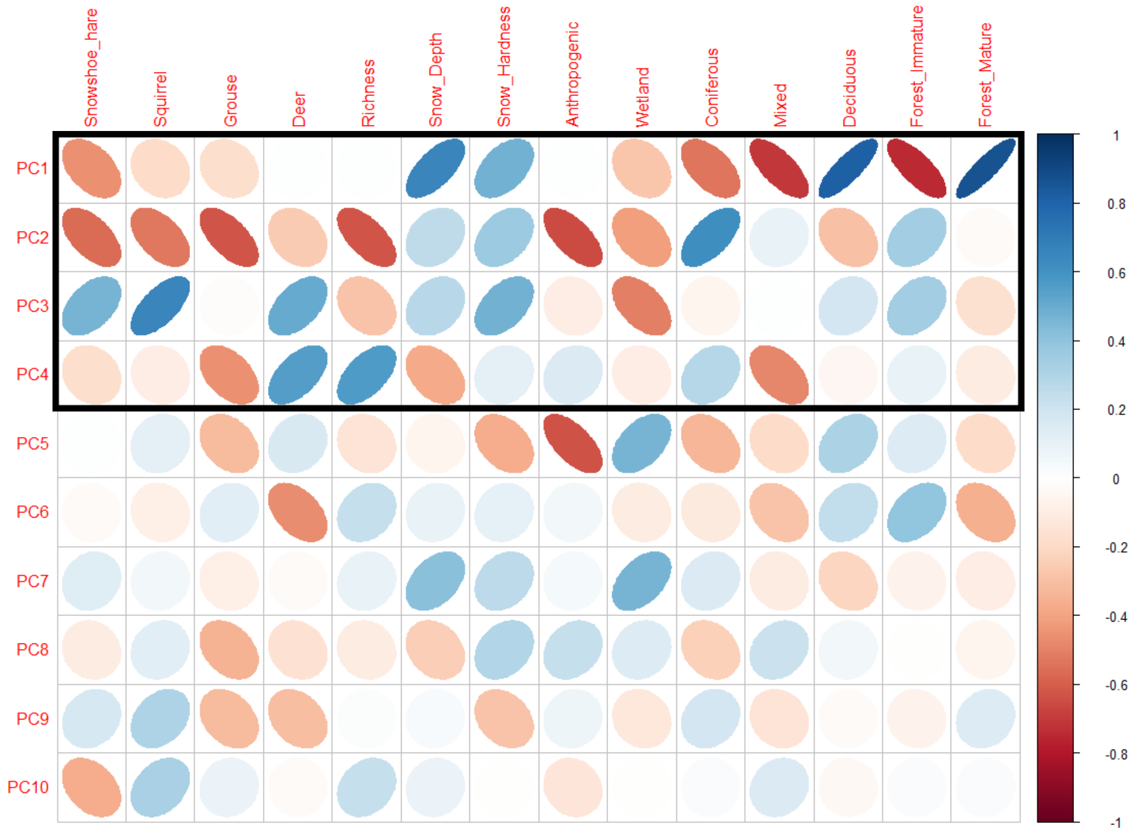

Figure S5. Correlation plot between principal components and habitat covariates for snowmobile routes surveyed for bobcat and lynx snow tracks from 2016 to 2018 during the months of January to March in Ontario, Canada. We used the first 4 principal component axes in the subsequent analyses. They explained 69.3% of the variance of these 14 habitat characteristics. We chose these 4 first axes because we wanted to reduce the number of predictors, and the interpretation of the remaining axes was difficult and some of these only had loadings associated to a single habitat characteristic (e.g. PC5 and PC6).

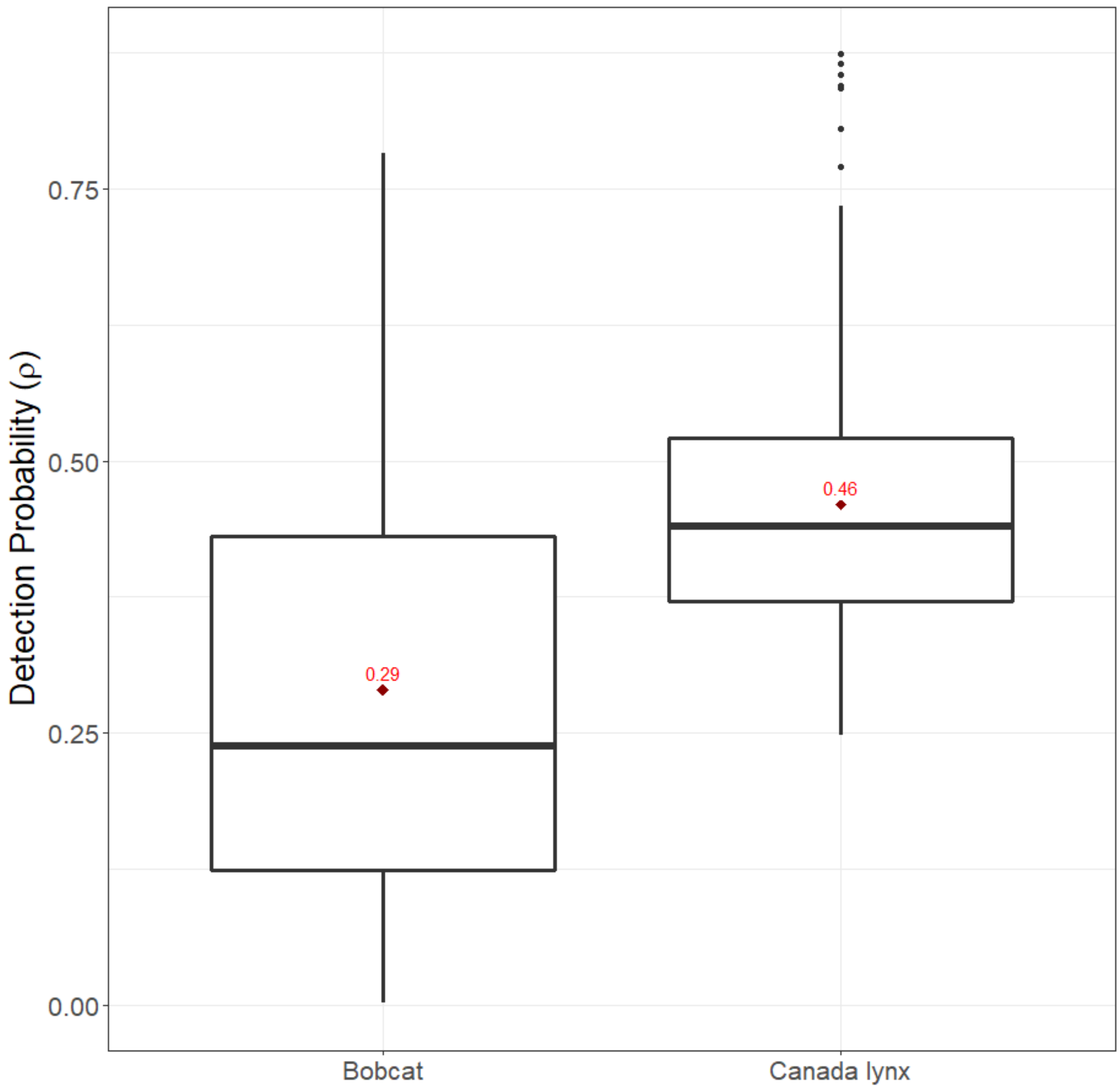

Figure S6. The probability of detection (ρ) for bobcat and lynx on snowmobile routes. Bobcats are generally less likely to be detected over our study area. In fact, they are on average 1.59 times less likely to be detected compared to lynx.

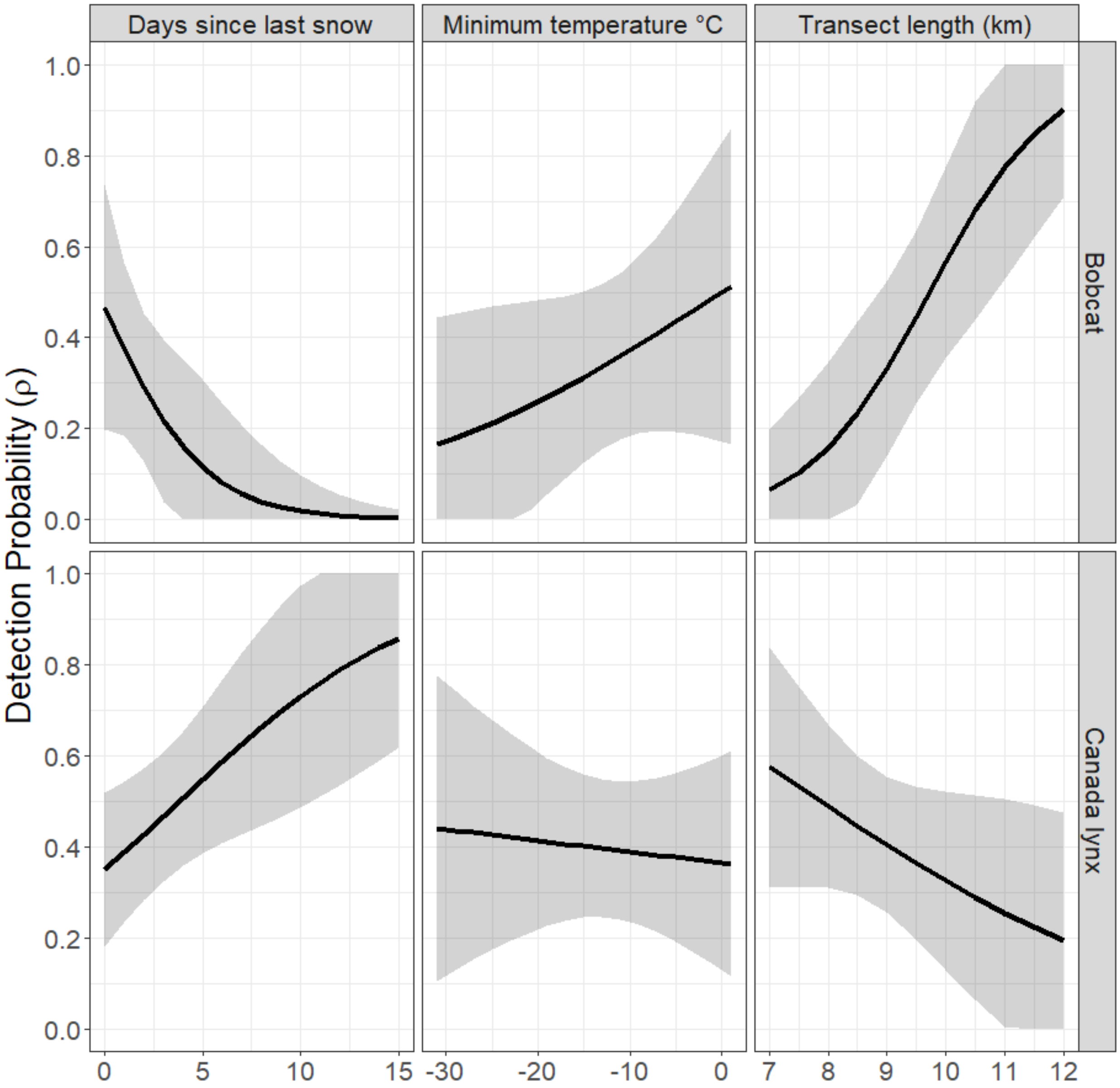

Figure S7. The probability of detection in accordance with observation-level predictors of bobcat and lynx occupancy. The minimum temperature did not influence detectability, but the number of days since the last snowfall influenced the detection of the lynx and the length of the snowmobile route influenced bobcat detection. The shaded areas are the 95% confidence interval (ρ ± Standard error).

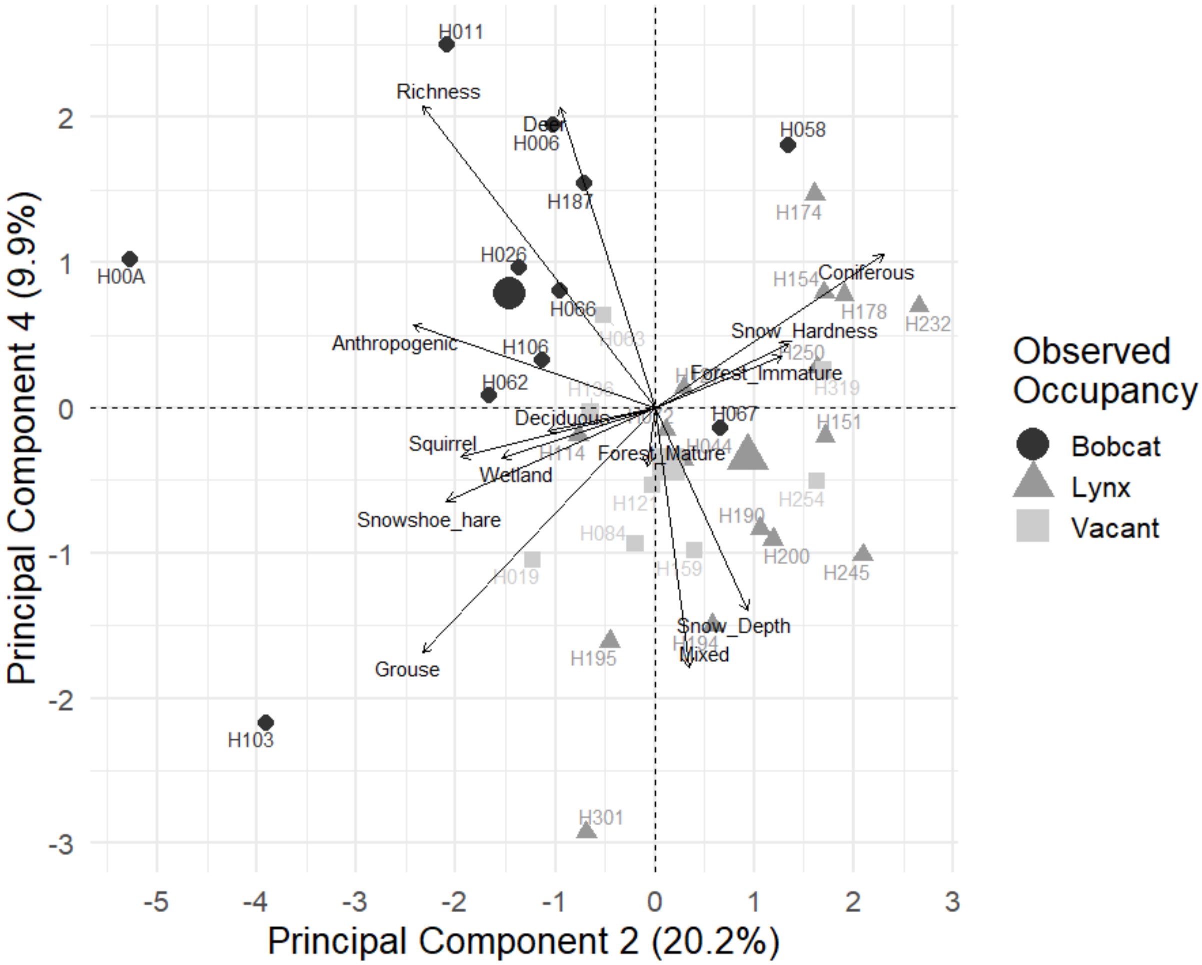

Figure S8. Biplot of principal component 2 and 4 for habitat predictors of bobcat and lynx occupancy.

Chapter 7: Synthesis

The general objective of my thesis was to further our understanding of the causes of the southern range dynamics of a unique cold adapted species the Canada lynx (*Lynx canadensis*) in the face of anthropogenic change and invading competitors. To do so, in chapter 2, I first investigated the potential drivers of the southern range limit of the Canada lynx. There are many detailed and thorough reviews of this topic (Aubry *et al.* 2000, Murray *et al.* 2008, US Fish and Wildlife Service, 2017). The diet of the Canada lynx is predominantly snowshoe hare (O'Donoghue *et al.* 1998) and consequently its population dynamics mimic closely the decadal fluctuation of the snowshoe hare population across its range (Poole 2003). The major factor that limits lynx persistence in the southern periphery is the low density of snowshoe hare. Lynx can only persist in areas where hare density is above 0.5 hares/ha (Hodges 2000a, Ruggiero *et al.* 2000b, Squires and Ruggiero 2007, Maletzke *et al.* 2008, Zahratka and Shenk 2008, Hodges *et al.* 2009, Berg *et al.* 2012, Ivan *et al.* 2014). Another main aspect of a viable southern lynx population is its connectivity to core boreal populations, since the periphery acts as a population sink as part of a larger metapopulation (McKelvey *et al.* 2000, Schwartz *et al.* 2002).

The southern range dynamics of the Canada lynx

In chapter 3, I estimated the extent of the southern range of the Canada lynx in Ontario between 1948 and 2014 using harvest records and tested several hypotheses of range dynamic that I documented in chapter 2. Unfortunately, I did not have a long-term dataset on snowshoe hare population dynamics, consequently I did not have enough power to test this driving factor. However, I was able to use independent records of Canada lynx harvested in the boreal forest to test the metapopulation theory (US Fish and Wildlife Service 2017). I found that the dynamics of the southern lynx range was best explained by the dynamics of the boreal lynx populations and connectivity to the boreal forest. During peak lynx years in the boreal forest the southern range expands in the following year in areas that are closer to the boreal forest and that have deep winter snow.

I also found that the southern range of the Canada lynx in Ontario has not changed substantially since large fluctuations before the 1970s. These results are in inconsistent with what had been previously found by Koen *et al.* (2014a), but this early study did not account for harvest effort. In addition, my study had data from 1948 to 2014 while theirs only had data from 1972 to 2010. The later period in our analysis is where the most recent expansion had happened. However, we did find a similar range contraction between 1970 and the 1990s as Koen *et al.* (2014a) indicated.

The southern range of the lynx between 1990 and 2014 has not contracted in Ontario but appears to have expanded. This is in contradiction to observed declines in the Great Lakes states and in the northeast United States (Michigan, New York, Vermont, New Hampshire; McKelvey 2000). It is quite established that many of these areas no longer have stable resident lynx populations (US Fish and Wildlife Service 2017). And we do know that the lynx range has contracted from its historical range (Laliberte and Ripple 2004). However, in Ontario, if we compare the southern range to its lowest point in the 1950s, the lynx seems to be fluctuating but stable, we will likely see another ephemeral contraction of the range in the east in Ontario quite soon.

The bobcat, a competitor?

There is ongoing debate whether the bobcat competes with the lynx for resources or by direct interference competition (Parker *et al.* 1983, Hoving *et al.* 2003, Peers *et al.* 2013, Gooliaff and Hodges 2018, Gooliaff *et al.* 2018, Newbury and Hodges 2018, Scully *et al.* 2018). In Ontario, the bobcat range has been expanding and may pose a threat to the Canada lynx in the form of competition and introgressive hybridization (Homyack *et al.* 2008, Koen *et al.* 2014b). However, we did not know how bobcats are expanding into northern Ontario and how populations are connected throughout the Great Lakes Region. We also did not know whether the bobcat and the Canada lynx are occupying the same geographical space and whether they are using similar resources in areas of overlap. Consequently, I investigated both these aspects in Chapter 5 and 6.

In chapter 5, I determined what landscape characteristics impeded or facilitated the northward range expansion of the bobcat into lynx territory. I used genetic information genotyped from fur samples collected from bobcat pelts to test several connectivity models. I found that the additive influence of the Great Lakes, forest stands with either low or high canopy cover and deep lake-effect snow have disrupted bobcat gene flow, whereas intermediate forest cover has facilitated gene flow. Important pathways across the Great Lakes into lynx territory were through the Lower Peninsula of Michigan over the Straits of Mackinac and the St. Mary's River. These pathways are important routes for bobcat range expansion north of the Great Lakes. The bobcat seemed to have been limited from invading lynx territory through the Upper Michigan Peninsula, but there did not seem to be any restrictions for expansion from Minnesota into Canada west of Lake Superior.

In chapter 6, I investigated an area of range overlap in Ontario that I found using fur harvest records from 2000 to 2005. This gave me the opportunity to investigate bobcat and lynx spatial patterns and habitat use on the north shore of Lake Huron in Ontario, Canada. Between 2016 and 2018, I surveyed snowmobile routes for their snow tracks over 3 winters and found that bobcat and lynx tracks were never on the same survey route. Bobcats occupied areas that had high habitat heterogeneity whereas lynx occupancy areas that were generally homogenous with high coniferous cover and low prey diversity. My results fit with the common assumption of the generalist and specialist natures of the bobcat and lynx, respectively. These findings suggested that the bobcat had invaded former lynx territory after these areas became vacant due to land use modification.

In the scientific literature there is no evidence of interference competition between these well studied and documented species. In my own fieldwork while I was trapping and tracking these cats in the Algoma and Sudbury district in Ontario, I noticed a quick transition between areas occupied by lynx and bobcat. I never found tracks of bobcat and lynx on the same routes, but there was a location that I captured a picture of a bobcat in November 2017 on trail camera; in this very same location, during each winter I also found tracks of Canada lynx in the winter months, but not the fall months. Contrarily, there were no signs of bobcat during the winter. Consequently, signs of these species in this location were never during the same season. There is likely a seasonal aspect of the habitat uses of both species that I may have missed, since I only sampled in winter. This aspect of seasonality of habitat use has been documented in other studies and may be an additional case that needs to be investigated in the context of competition (Scully *et al.* 2018, Morin *et al.* In Press). There were also areas during standardized field collection where I found bobcat tracks and then found lynx tracks incidentally off path approximately 3 kilometers away on the same day. A possible explanation could be that lynx are less likely to use trails in areas that have a certain frequency or density of human disturbances and at this same level of disturbance the bobcat is unaffected since it is generally found in areas that are more disturbed across its entire range compared to the lynx (Peers *et al.* 2013).

Direct evidence of competition so far between these species is quite limited. Previously the idea of competition was first mentioned by Peterson and Downing (1952). It was later triggered by anecdotes from Parker *et al.* (1983) and then the bioclimatic analysis by Peers *et al.* (2013) that indicated that these species were competing at a continental scale. More recent analyses indicated that these species avoided each other in space or time, and this is could be a strategy that reduces competitive interaction and allows coexistence (Armstrong and McGehee 1976). For instance, Gooliaff *et al.* (2018) found that the bobcat was restricted to the south or at lower elevation, while the lynx was found in the interior or at higher elevation in the province of British Columbia, Canada. Scully *et al.* (2018) found that lynx avoided camera sites where bobcats were present. Some have reasoned that the potential for competition is high, because the species are closely related, morphologically similar, and use similar resources (Peers *et al.* 2013). Also, these species do infrequently hybridize (Homyack *et al.* 2008, Koen *et al.* 2014a, Schwartz *et al.* 2004).

In contrast, coexistence between lynx and bobcat also seems possible, because they have very different dietary strategies and no demographic impact has ever been reported by one species on the other in an area of sympatry (Newbury *et al.* 2019). Therefore, spatial segregation may also be evidence of coexistence, since they use very difference resource that are segregated spatially. I found spatial and habitat segregation between these species and this further indicates that lynx and bobcat can coexist simply because they use very different resources. The assumption that they may compete just because they are closely related seems quite unwarranted (Peers *et al.* 2013). It simply seems that the bobcat cannot persist in areas where lynx occur, while the lynx cannot persist where bobcat occur and this has nothing to do with competition, but simply a result of limitation by resources.

The fact that both species do not occur together and that their habitats are generally quite different points more towards the backfilling of modified habitat by the bobcat after the lynx vacated these areas because it could no longer persist in them (de Vos 1964). Naturalists had observed this pattern during earlier periods (Hoving *et al.*2003). However, there aren't many areas where this has happened in recent times (exception: Parker *et al.* 1983, de Vos and Matel 1952, de Vos 1964). During the middle of the last century, this pattern had previously been observed in the Great Lakes regions, but mostly in Ontario (de Vos and Matel 1952, de Vos 1964). They indicated that forestry practices had altered the habitat of the lynx to the point where it could no longer persist and that over trapping may have also led to the contraction of the lynx range and the bobcat was able to then prosper in this habitat. Consequently, the anthropogenic change was causal, rather than competition. One important aspect relevant to exploring potential competition is that bobcats are still quite rare in Ontario. The number of bobcats harvested in Ontario had only reached over 100 in 2011, whereas earlier there were generally less than 50 bobcats harvested each year across the whole province.

Finally, Morin et al (2019) reviewed whether there is any evidence of potential for competition between these two species. They tabulated habitat selection of each species for all Johnson orders of selection (Johnson 1980). They found that no study has shown overlap and in addition both species also selected different resources at higher Johnson orders (coarse scale). They concluded that because habitat selection is conditional on higher orders of selection, then this would indicate that these species do not select for similar resources, therefore the potential competition between these species is less likely than previously believed.

Conclusion

I found that the southern range of the Canada lynx was driven by connectivity to core boreal lynx populations and when these populations reach their peak, individual disperse south and colonize areas outside of the boreal forest. In March 2019, a Canada lynx was found in Harbor Beach, Michigan, over 300 km from the boreal forest. At the same time lynx in Maine were increasing in numbers and lynx in New Brunswick were thriving. On the other side of the continent, lynx in

British Columbia seem to be stable. However, it seems that southern populations that are over 100 km away from the large tracts of boreal forest will likely always have unstable lynx populations, simply because they are reliant on transient lynx that disperse to the periphery and further south after peak years in the boreal forest.

In the Lower 48 US states, the Canada lynx was originally listed as ‘threatened’ because of habitat loss due to forestry practices. On January 11, 2018, the U.S. Fish and Wildlife Service announced that its recommendation to remove Endangered Species Act protections for the threatened Canada lynx in the Lower 48 States. They concluded that these lynx populations have stabilized, because the risk of decline due to habitat loss has largely been mitigated. However, this recommendation seems quite surprising since these southern populations are disjunct from the larger boreal core lynx population in the north and will likely always be unstable. In addition, many of these southern populations do not have high snowshoe hare densities well above 0.5 hare/hectare that would allow a persistent resident lynx population. Removing the current protection status of the lynx can only further limit the natural ability of these southern populations to be rescued as part of a larger metapopulation. Consequently, downgrading its protection status is in contradiction to what we currently know about the lynx in these areas and what we know generally about lynx ecology. The hope is that US state governments maintain current forestry practices that have mitigated the past habitat loss of the Canada lynx. Fortunately, there are also groups that are preserving large tracks of land that connect these populations as a larger network of protected areas that spans from Yellowstone to Yukon (y2y.net) and also the Adirondacks to Algonquin (a2acollaborative.org).

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APPENDIX A

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