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Interacting effects of climate and biotic factors on mesocarnivore distribution and snowshoe hare demography along the boreal-temperate ecotone

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INTERACTING EFFECTS OF CLIMATE AND BIOTIC FACTORS ON MESOCARNIVORE DISTRIBUTION AND SNOWSHOE HARE DEMOGRAPHY ALONG THE BOREAL-TEMPERATE ECOTONE

A Dissertation Presented

by

ALEXEJ PEDER KELLY SIRÉN

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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Department of Environmental Conservation
Wildlife, Fish and Conservation Biology

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DEDICATION

I dedicate this dissertation to all my friends up north.

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ABSTRACT

INTERACTING EFFECTS OF CLIMATE AND BIOTIC FACTORS ON MESOCARNIVORE DISTRIBUTION AND SNOWSHOE HARE DEMOGRAPHY ALONG THE BOREAL-TEMPERATE ECOTONE

MAY 2020

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The motivation of my dissertation research was to understand the influence of climate and biotic factors on range limits with a focus on winter-adapted species, including the Canada lynx (*Lynx canadensis*), American marten (*Martes americana*), and snowshoe hare (*Lepus americanus*). I investigated range dynamics along the boreal-temperate ecotone of the northeastern US. Through an integrative literature review, I developed a theoretical framework building from existing thinking on range limits and ecological theory. I used this theory for my second chapter to evaluate direct and indirect causes of carnivore range limits in the northeastern US, using data collected from 6 years (2014–2019) of fieldwork. My third chapter again used this theory and classical understanding of density-dependence to evaluate factors influencing snowshoe hare populations along their trailing edge in the northeastern US. Finally, for my fourth chapter, I used the model outputs from the second chapter to compare current and future distributions based on causal and correlational frameworks given projected changes in snowpack and forest biomass.

In Chapter 1, I revisited a long-standing theory on range limits, often credited to Charles Darwin (1859), that posits that harsh climate forms upper distributional limits and biotic interactions form lower limits (hereafter Range-Limit Theory; RLT). I proposed an extension to this theory (Interactive Range-Limit Theory; iRLT): positive biotic factors can ameliorate harsh climate along upper edges, whereas climatic stress can mediate negative biotic interactions along lower limits. To evaluate support for RLT and iRLT, I performed an integrative review of 290 papers, focusing on mammalian carnivores and herbivores of North America. Although I found support for both theories, there was more evidence for iRLT. Harsh climate (e.g., deep snow) had a limiting effect on populations along upper limits, yet the availability of prey or habitat ameliorated negative effects. Conversely, harsh climate had a positive effect for populations along lower limits as it mediated negative biotic interactions. As hypothesized, I also found clear differences among trophic levels; carnivores were only limited by competition whereas predation or parasitism imparted a greater influence on herbivores along lower limits. I discuss how these trophic differences may result in variable dynamics along range limits. This review (Sirén & Morelli, 2019) provides a theoretical framework for evaluating the impacts of climate and land use change on species distributions.

In Chapter 2, I utilized the theoretical framework developed in Chapter 1 (iRLT) to evaluate the direct and indirect effects of snow and prey/habitat availability on carnivores along upper and lower range limits in the northeastern US. I evaluated two hypotheses of iRLT using occupancy and causal modeling frameworks based on data collected over a 6-year period (2014–2019) of 6 carnivore species across broad latitudinal (42.8–45.3°N) and altitudinal (3–1451 m) gradients. I found that snow directly limits populations at high altitudes and higher latitudes, but prey or habitat availability can influence range dynamics, supporting my first hypothesis. For example, bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) were limited by deep snow and long winters along upper edges but the availability of an abundant prey base, including temperate and boreal species, had a strong positive effect, especially for bobcats. Conversely, snow had a strong positive effect on the lower limits of Canada lynx and American marten. For lynx, the indirect effect of snow was strongest and countered the negative effect of competition, especially with the phylogenetically similar bobcat, supporting the hypothesis that climate mediates competition between similar species and forms lower range limits. I also found prey and habitat availability to have strong direct and indirect effects for lynx and martens, indicating that several factors are important for populations along low elevation and southern edges. This study, submitted to the journal *Ecography*, supports iRLT and underscores the need to consider direct and indirect mechanisms for studying range dynamics and species' responses to global change.

In Chapter 3, I evaluated the trophic hypothesis of iRLT using snowshoe hares – an iconic herbivore of the boreal and boreal-temperate forests of North America. I hypothesized that density-dependent predation, elicited by bottom-up effects, plays an important role for herbivores along lower range limits. I hypothesized that limiting resources – in this case habitat availability – leads to a low-density refuge that allows herbivores to persist undetected along lower range limits, escaping predation and parasitism. I collected field data on distribution, population density and fluctuations, habitat use, survival, and reproduction of snowshoe hares to test the hypothesis that resource-mediated density dependence determines, in part, species' persistence along trailing edges. From a 6-year study (2014–2019), I found that variability in snow and resource availability affects density and population fluctuations and leads to trade-offs in survival and reproduction for snowshoe hare populations in the northeastern US. Hares living in resource-poor environments had lower but stable population density, low reproductive effort, yet higher survival compared to populations living in resource-rich environments. I suggest that density-dependent dynamics, elicited by resource availability, provide hares a unique survival advantage and partly explains persistence along their trailing edge. I hypothesize that this low-density refuge from predation and parasitism occurs for other prey species along trailing edges, but the extent to which it occurs is conditional on the quality of matrix habitat. Given that species ranges are shaped by several factors other than climate, including biotic and intraspecific factors, I advocate for a more careful examination of factors influencing populations along trailing edges to better inform conservation and management decisions.

In Chapter 4, I compared correlative and causal approaches for modeling species distributions using the theoretical framework I developed in Chapter 1 and model outputs from Chapter 2. Specifically, I compared current (2014–2019) and future (2080) distributions of ecologically important mammalian carnivores and competitors under a high-emission scenario (RCP8.5) of projected snow and forest biomass change using causal and correlational models and iRLT. My hypothesis that climate-mediated competition and bottom-up processes would result in differential distributions, both in the current and future periods was supported. My comparative analysis indicates that a causal framework, steeped in ecological theory, should be used to predict species' response to global change.

Results of my research advances ecological theory relating to the causes of range limits and factors influencing trophic levels and provides an applied framework to understand and predict current species distributions and population dynamics. Identifying the direct and indirect effects of climate and land use change on species' ranges provides a mechanistic framework to predict how global change will redistribute populations across the globe. My research was largely shaped by stakeholder needs and stakeholder engagement. As such, results from my research are currently being used to inform conservation and management decisions in the northeastern U.S., including the Canada lynx delisting process, land conservation for American marten, and habitat management for snowshoe hares. My dissertation research has also inspired agency personnel to consider a community-wide approach to single-species management. This perspective, in addition to my theoretical contribution, can be used to proactively conserve and manage populations that are currently and/or predicted to be negatively impacted by climate change.

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CHAPTER 1

INTERACTIVE RANGE-LIMIT THEORY (IRLT): AN EXTENSION FOR PREDICTING RANGE SHIFTS

1.1 Introduction

Understanding how and why geographical range limits form and change over time is a long-standing inquiry of biogeographers and ecologists. An enduring hypothesis, dating back to Darwin (1859), posits that high latitude/altitude range limits are formed by stressful abiotic environments (e.g., cold climates), whereas lower limits are set by biotic interactions (e.g., competition, predation). This hypothesis is a major tenet of biogeography and has been subsumed in various definitions of the niche in ecology (Brown, Stevens, & Kaufmnan, 1996; Connell, 1961; Dobzhansky, 1950; MacArthur, 1984). It has undergone a recent resurgence given its potential to better understand impacts of global change on species distributions (Anderegg & HilleRisLambers, 2019; Dvorský, Macek, Kopecký, Wild, & Doležal, 2017; Louthan, Doak, & Angert, 2015; Normand et al., 2009).

However, after more than a century of theoretical and empirical groundwork, there is little consensus on the extent to which abiotic and biotic factors (see Box 1 for definitions) determine range limits and how this varies by distributional edge position (Alexander, Diez, Usinowicz, & Hart, 2018; Godsoe, Jankowski, Holt, & Gravel, 2018; Louthan et al., 2015). Although many studies indicate that high-latitude/altitude (hereafter upper) limits are formed by abiotic factors (see papers in Hargreaves et al., 2014), biotic factors can mediate abiotic stress along upper limits (Ettinger & HilleRisLambers, 2017; Pitt, Larivière, & Messier, 2008). Moreover, few studies have shown that low-latitude/altitude (hereafter lower) limits are caused by biotic interactions (Cahill et al., 2014; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). Potential explanations are that biotic interactions only have influence at local scales (Soberón, 2007; Wiens, 2011), or that the scant availability of biotic data at broad spatial scales (e.g., distribution of competitors) precludes meaningful inference (Wisz et al., 2013). Another possibility is that correlations between abiotic and biotic factors confound interpretations of the importance of either along range limits (Godsoe, Franklin, & Blanchet, 2017; Sexton, McIntyre, Angert, & Rice, 2009; Westoby, Kunstler, Leishman, & Morgan, 2017). Thus, it can appear that abiotic factors restrict populations along lower limits despite an underlying biotic constraint; the opposite process can also occur along upper limits. This correlation is rarely tested, yet it could provide important insight into the interactive nature of factors that form range limits and allow for predictions that will be valuable to conservation in the face of global change.

Recent scholarship (e.g., Godsoe, Jankowski, et al., 2017) has emphasized the need to integrate ecological theory to better understand how and under what conditions biotic factors influence range limits, especially considering increasing threats from climate change, habitat conversion, and species invasions (Guisan et al., 2013; Parmesan, 2006). To this end, we propose an expansion of current thinking on range limits – interactive range-limit theory (iRLT) – which makes predictions for range limits and shifts. We begin by summarizing previous hypotheses and models on range limits to frame iRLT. We use a conceptual model to illustrate that range limits and shifts are the result of an interaction between abiotic and biotic factors, and provide evidence from an integrative review, primarily focused on North American mammals. We also investigate the evidence for how biotic interactions vary by trophic level and how this may create divergent range patterns for mammalian carnivores and herbivores. We end by outlining limitations and future directions of iRLT.

Box 1. What is the difference between a biotic interaction and a biotic factor?

The terms 'biotic interactions' and 'biotic factors' are commonly used in range-limit studies. However, they can have different meanings which can cause confusion. **Biotic interactions** are defined as direct intraspecific or interspecific interactions (e.g., competition, predation, mutualism) that have a negative, neutral, or positive effect on a focal species' distribution or abundance and are typically limited to interactions within or between adjoining trophic levels (Anderson, 2017; Andrewartha & Birch, 1954; Krebs, 1972). **Biotic factors**, on the other hand, is a more general term that also includes **unlinked biotic factors** (density-independent) that are not significantly consumed or contested and have influence at broad spatial and temporal scales (Anderson, 2017; Peterson et al., 2011; Soberón, 2007). These include 'unlinked biotic predictors' (e.g., habitat structure), 'composite biotic predictors' (e.g., habitat type), and 'unlinked biotic interactors' (e.g., distribution of a food resource) that can span multiple trophic levels and also have positive, negative, or neutral effects on a focal species (Anderson, 2017; Peterson et al., 2011). In some cases, positive or negative associations with unlinked biotic predictors/interactors (e.g., habitat type) have been used as proxies for biotic interactions, due to the paucity of interaction data at broad spatial scales (Morales-Castilla, Matias, Gravel, & Araújo, 2015; Wisz et al., 2013); when this was evident, we included interpretations provided by studies. We refer to biotic interactions and unlinked biotic factors using the definitions described above and use biotic factors when studies combined these categories or were vague in their usage of them.

1.2 An overview of range-limit theory (RLT)

Despite numerous theoretical and empirical investigations of range limits over the past centuries, there is not a clear definition of "range-limit theory". However, empirical models and hypotheses on ecological causes of range limits tend to group under three categories (Louthan et al., 2015; Sexton et al., 2009; Srinivasan, Elsen, Tingley, & Wilcove, 2018). The first category only considers abiotic factors to form range limits (Table 1.1). These include species distribution models which evaluate correlations between abiotic variables and empirical data or published physiological tolerances (Araujo & Peterson, 2012). These models assume that the geographic distributions are manifestations of a range of environmental conditions (i.e., the fundamental niche; Hutchinson, 1957). There are other abiotic-only hypotheses of range limits that are not necessarily based on niche theory (e.g., Climatic Variability Hypothesis). Some abiotic-only hypotheses are edge-specific such as that proposed by Darwin (1859) and derivatives thereof (Table 1.1) that posit abiotic stress forms upper limits (Louthan et al., 2015; Normand et al., 2009).

A second group considers only how biotic factors or interactions form range limits (Table 1.1). This includes the hypothesis that biotic interactions form lower limits originating from Darwin (1859) (Table 1.1). Another group of biotic models hypothesize that abundance, fitness, and genetic diversity decrease outwards from the center of a species geographic range (Table 1.1; Abundant-centre model and others) due to exogenous (e.g., patchy habitat) and/or endogenous (e.g., limited dispersal ability) factors (Brown, 1984; Carter & Prince, 1981). Like Darwin’s hypothesis on range limits, the spatial patterns of these models are generally assumed to occur in nature, but evidence supporting their existence is equivocal (Pironon et al., 2017).

The third category for understanding causes of range limits explores interactions between abiotic and biotic factors. The Stress-Gradient Hypothesis (SGH) (Callaway et al., 2002) and Condition-Specific Competition (CSC) (Nagamitsu, Yamagishi, Kenta, Inari, & Kato, 2010) are two common approaches; the former has been applied primarily to plants and the latter to animals (Table 1.1). Both predict that environmental stress mediates biotic interactions across a gradient of conditions. They are commonly evaluated in altitudinal studies (Ettinger & HilleRisLambers, 2017; Twomey, Morales, & Summers, 2008) with some focus on geographical limits (Malenke, Newbold, & Clayton, 2011; Meier, Edwards, Kienast, Dobbertin, & Zimmermann, 2011). They are also consistent with the Darwin’s hypothesis on range limits, assuming abiotic and biotic factors have greater influence on either end of range limits, yet these assumptions are not explicit. One primary difference is the SGH predicts that positive biotic interactions are influential in stressful environments and negative biotic interactions in mild climates. CSC is similar to the SGH but, as the name implies, is limited to competitive interactions and does not predict positive biotic interactions in abiotically stressful environments.

In combination, these hypotheses comprise the commonly referenced (but previously undefined) ecological component of “range-limit theory” (Connallon & Sgrò, 2018; Hargreaves et al., 2014; Johansson, Frisk, Nemomissa, & Hylander, 2018; Louthan et al., 2015; Sexton et al., 2009). Hereafter, we refer to “range-limit theory” as RLT, with an emphasis on the long-standing hypothesis posited by Darwin (1859) and others since then (Table 1.1).

1.3 Interactive range-limit theory (iRLT)

To formalize the interactive nature of abiotic and biotic factors along range limits that has been highlighted in previous research (Godsoe, Franklin, et al., 2017; Wisz et al., 2013), we propose an expansion of RLT, interactive range-limit theory (iRLT), that incorporates interactions among abiotic and biotic factors. iRLT produces the primary predictions of RLT (Table 1.2; Fig. 1.1a), with some major additions. In agreement with RLT, abiotic factors are more influential along upper limits of a species' range. But iRLT hypothesizes that biotic factors can ameliorate abiotic conditions and moderate range-limit dynamics (Table 1.2; Fig. 1.1b). Similarly, biotic interactions are still predicted to be more important along lower limits, but iRLT hypothesizes that abiotic factors can mediate biotic interactions and thus range limits (Table 1.2; Fig. 1.1b). We predict that the most pronounced shifts on either edge of a species' distribution occur when abiotic and biotic factors oppose each other (i.e., marked expansion occurs along upper limits following a decrease of negative abiotic factors and a simultaneous increase of positive biotic factors, with the opposite pattern for lower limits).

Consider the following scenario of range dynamics along an upper limit. A population of Species A is limited by an abiotic factor. For example, exposure to cold reduces survival and lowers population growth rates, creating the upper limit of the species range, as predicted by RLT (Fig. 1.1c). Accordingly, range expansion will follow periods of warming, whereas contraction will occur if temperatures decrease, indicating that climate ultimately forms range limits. Southern pine beetles in North America provide a contemporary example of expansion along upper limits due to anthropogenic warming (Lesk, Coffel, D'Amato, Dodds, & Horton, 2017). An extreme version of contraction occurred during glacial periods in North America, where ice forced populations to retreat downslope and southward (Lomolino, Riddle, & Whittaker, 2016).

iRLT, on the other hand, accounts for the complexity that spatial and temporal variation creates along range limits. A particularly beneficial biotic factor can ameliorate the negative influence of a harsh environment and allow for population persistence along high range limits (Fig. 1.1d). For instance, populations of Species A may persist along upper range limits despite low winter temperatures because there is optimal habitat or abundant food resources that enable individuals to thermoregulate more easily and increase survival. However, if these positive biotic factors diminish, survival will decrease and result in contraction along upper limits (Fig. 1.2a). Further, if there is a coincident increase in cold temperature, contraction will be especially pronounced. Conversely, where negative abiotic factors lessen and positive biotic factors increase, range expansion is fueled along upper limits for some species (Fig. 1.2b) (e.g., Elmhagen et al., 2017). Range expansion along leading range edges in response to modern climate change is perhaps the most obvious example.

Now consider a population of Species A along its lower range margin, where, according to RLT, biotic interactions (e.g., competition) are considered the primary determinant of range limits (Table 1.2; Fig. 1.1e). Although Species A is limited by competition, it has greater tolerance for a stressful abiotic factor (e.g., cold temperature) than its competitor along lower range margins. Thus, iRLT predicts that abiotic stress can act as a buffer by reducing the fitness of the competitor but not Species A (Fig. 1.1f). However, when temperatures warm, the focal species becomes exposed to environments that are suitable for its competitor, resulting in range contraction of the focal species (Fig.

1.2c). Conversely, range expansion will occur if the abiotic factor intensifies relative to the strength of the biotic interaction (Fig. 1.2d).

Thus, the simplest case of iRLT, in the absence of interactive effects, produces the same predictions as RLT. However, the expectation is that interactive effects are common and affect many species on both edges of their ranges. We next set out to test this assumption.

1.4 Review of evidence for iRLT

1.4.1 Context

To provide evidence of the applicability of iRLT and to determine the extent to which biotic interactions varied by trophic level, we reviewed literature based on a specific set of criteria (see Text A1, Tables S1–S2; Appendix A). First, we looked for evidence of RLT: that studies at upper limits would show negative impacts of abiotic factors, and that studies at lower limits would show negative impacts of biotic factors (Table 1.2). We further predicted, based on iRLT, studies of populations along upper limits would also document positive associations with biotic factors, whereas those along lower limits would detect positive associations with abiotic factors (Table 1.2). We used studies of mammalian carnivores and herbivores from North America with a focus on those occurring along the boreal-temperate (Goldblum & Rigg, 2010) and forest-tundra (Payette, Fortin, & Gamache, 2001) ecotones. We chose this region as many studies have been conducted along these ecotones over the past century (Eckert, Samis, & Lougheed, 2008), providing an opportunity to evaluate the extent to which abiotic and biotic factors influence range limits. Further, ecotones, in general, are considered ideal regions to evaluate the influence of abiotic factors (e.g., climate) on species distributions as they often coincide with range limits (Kupfer & Cairns, 1996). Our review spanned 5 taxonomic orders and provided a total of 15 families, 31 genera and 52 species (Table S1 in Appendix A).

1.4.2 Evidence for iRLT along high-latitude/altitude limits

In concert with RLT, abiotic factors often imposed a negative influence on upper range limits of mammalian carnivores and herbivores from North America along the boreal-temperate and forest-tundra ecotones (n = 61 studies, Table 1.3), with deep snow or cold temperatures often considered the limiting factors. On the other hand, unlinked biotic factors (Box 1) such as habitat or prey availability had a positive influence along upper limits; this interaction of a biotic factor lessening the negative impact of an abiotic factor is evidence in support of iRLT (n = 57 studies, Table 1.3). This pattern was evident for carnivores and herbivores (Table S3 in Appendix A) and for studies that only evaluated abiotic or biotic factors, instead of both (Table S4 in Appendix A). However, our review process may have inflated the number of studies that reported positive associations with unlinked biotic factors along high range limits (see bias assessment, Text A1 in Appendix A). Comparatively, there were fewer studies that found positive and negative associations with abiotic and biotic factors, respectively, along upper limits (Table 1.3). Limiting biotic factors were typically associated with food availability or habitat type (e.g., open tundra). Evidence for the impact of biotic interactions on upper limits was rare (n = 3 studies; Table 1.3); however, relatively few studies evaluated species interactions at broader spatial scales.

Finally, a subset of the papers in our review evaluated range shifts along upper limits (Table S5 in Appendix A). Most studies documented range expansion (n = 13), instead of contraction (n = 4) or stability (n = 1). The availability of habitat or prey often ameliorated the effect of negative abiotic factors. For instance, bobcats (*Lynx rufus*), normally snow-limited, can persist for years in deep snow locales along high-latitude limits if there are large or abundant prey (Litvaitis & Harrison, 1989; Major & Sherburne, 1987; Newbury & Hodges, 2018). A similar pattern has been inferred for other purportedly snow-limited carnivores, including fisher (*Pekania pennanti*) (Jensen & Humphries, 2019; McLellan, Vashon, Johnson, Crowley, & Vashon, 2018) and coyotes (*Canis latrans*) (Litvaitis & Harrison, 1989; Patterson, Benjamin, & Messier, 1998). These findings indicate, in support of iRLT, that populations may persist along upper limits if a positive biotic factor can overcome the negative abiotic impacts.

Range contraction along upper limits was often associated with a decline in positive unlinked biotic factors, such as prey and habitat availability. This dynamic occurred for felids (Litvaitis, Tash, & Stevens, 2006), ungulates (D’Eon & Serrouya, 2005), and small mammals (Wolff, 1996). A notable example is the southward contraction of white-tailed deer (*Odocoileus virginianus*) range in New England due to the loss of mature conifer forest – a habitat that provides refuge during deep snow winters (Simons-Legaard, Harrison, & Legaard, 2018). Another study documented a 240 km range contraction of southern flying squirrels (*Glaucomys volans*) along its northern limit during a shortage of tree seeds that coincided with a severe winter (Bowman, Holloway, Malcolm, Middel, & Wilson, 2005). However, the authors found that these populations persisted during harsh winters when seeds were especially abundant. A similar food-related shift in abundance was also observed for two mouse species (*Peromyscus spp.*) along an altitudinal gradient in the Appalachian Mountains (Wolff, 1996).

Range expansion along upper limits was especially evident when a negative abiotic factor decreased along with a corresponding increase of positive unlinked biotic factors (Dawe & Boutin, 2016; Lavoie et al., 2009). Some of the best examples include the northward expansion of opossum (*Didelphis virginiana*) and raccoons (*Procyon lotor*) in response to increasing food availability in conjunction with warming climate (Kanda, Fuller, Sievert, & Kellogg, 2009; Larivière, 2004; Pitt et al., 2008). Additionally, experimental work at local scales indicates abundant forage can buffer the negative effects of harsh climate for mule deer (*Odocoileus hemionus*) (Baker & Hobbs, 1985) and New England cottontails (*Sylvilagus transitionalis*) (Weidman & Litvaitis, 2011). These studies support the iRLT prediction of range expansion along upper limits, where the strength of biotic factors ameliorate harsh abiotic conditions (Fig. 1.2b).

There are some studies where biotic interactions were considered the direct limiting factor, or complex interactions between abiotic and biotic factors formed upper limits. For instance, predation rates were higher in open tundra for snowshoe hares (*Lepus americanus*) along its northern range limit in Canada (Barta, Keith, & Fitzgerald, 1989). Consequently, this species has benefitted from the northward expansion of shrubs in the arctic tundra (Tape, Christie, Carroll, & O'Donnell, 2016). Conversely, abiotic factors such as snow have been shown to increase the susceptibility of swamp rabbits (*Sylvilagus aquaticus*) and eastern cottontails to predation (Boland & Litvaitis, 2008;

Hillard et al., 2018), yet anthropogenic refuges can buffer losses for the latter species (Keith & Bloomer, 1993). Many of these studies, however, were not able to differentiate between direct and indirect causal effects.

1.4.3 Evidence for iRLT along low-latitude/altitude limits

Supporting iRLT, many species had positive associations with winter climate along lower limits (n = 46 studies, Table 1.3). Specifically, abiotic factors, such as snow or cold temperatures were positively correlated with the distribution of carnivores (n = 29 studies; Table S3 in Appendix A). A similar, but less pronounced, pattern prevailed for herbivores (n = 17 studies; Table S3 in Appendix A). Interestingly, unlinked biotic factors, such as prey or habitat availability, also had a strong and positive effect on range limits for both trophic levels (n = 49 studies, Table 1.3). This pattern was present for studies that only evaluated abiotic or biotic factors, instead of both (Table S4 in Appendix A). Comparatively, there were fewer studies that found negative associations with abiotic or unlinked biotic factors along lower limits (Table 1.3). In general, negative relationships with the latter were associated with anthropogenic habitat (e.g., roads) and considered a proxy of negative biotic interactions (e.g., predation; Beguin et al., 2013). Although fewer studies reported biotic interactions at the distributional scale, there were a higher number along lower limits, which is predicted by RLT (Table 1.3).

The few papers we found that evaluated shifts along lower edges primarily documented contraction (n = 14), yet some found expansion (n = 5), or stability (n = 2) (Table S5 in Appendix A). Similar to studies along high limits, range stability is likely more common than reported in the literature due to the bias against reporting negative results (Fanelli, 2012). Range contraction along lower limits was especially evident when positive abiotic factors reduced in strength relative to that of negative biotic factors. This occurred for carnivores when buffering from abiotic factors diminished and provided a competitive advantage for sympatric species (Elmhagen et al., 2017; Krohn, 2012). For example, a 175 km contraction along the southeastern edge of the snow-adapted Canada lynx (*Lynx canadensis*) range was associated with several decades of mild winters that enabled competitors to expand (Koen, Bowman, Murray, & Wilson, 2014; Peers, Thornton, & Murray, 2013). These patterns can occur locally at seasonal scales (Scully, Fisher, Miller, & Thornton, 2018) or geographically over longer time periods (Hoving, Joseph, & Krohn, 2003; Krohn, 2012). Range contraction was also observed for herbivores when the strength of an abiotic factor reduced, exposing populations to predation, disease, or parasitism. For example, recent studies indicate snowshoe hares experience higher predation rates and population declines when their white winter coats contrast with snowless environments (Wilson, Shipley, Zuckerberg, Peery, & Pauli, 2018; Zimova, Mills, & Nowak, 2016). Consequently, reduced snow duration over the past several decades is associated with range contraction along the snowshoe hare's southern limit (Burt, Roloff, & Etter, 2017; Sultaire, Pauli, Martin, Meyer, Notaro, et al., 2016) with future declines expected due to climate change (Zimova et al., 2016). These studies are in accordance with the iRLT prediction of range contraction along lower limits when the positive effect from an abiotic factor diminishes (Fig. 1.2c).

Range expansion was evident for carnivore populations along lower limits when abiotic factors were exceptionally strong; again, this dynamic occurred over short and long time scales (Hornocker & Hash, 1981; Krohn, 2012). This is well-illustrated by the historical ranges of extant species such as American marten (*Martes americana*) whose southern limit extended farther south in the northeastern United States during the Little Ice Age (Krohn, 2012). Expansion was also associated with the emergence of positive unlinked biotic factors (e.g., habitat availability); however, this occurred within the range of environmental conditions that suited the focal species but not its competitors (Hoving et al., 2003; Kelly, Fuller, & Kanter, 2009; Simons-Legaard, Harrison, & Legaard, 2016). Most of the latter examples occurred over longer time scales and were attributed to habitat availability. This dynamic indicates that a number of conditions may be required for range expansion along lower limits (Anderson et al., 2009; Hoving, Harrison, Krohn, Joseph, & O'Brien, 2005; McCann & Moen, 2011). Indeed, our review indicates that the ratio of positive abiotic to positive biotic factors along lower edges was relatively equal (46:49) compared to upper limits (Table 1.3). A common theme of these studies was that a strong abiotic factor was required for range expansion along lower limits.

Several authors indicate that a suite of complex interactions form lower limits. For instance, Belding's ground squirrels (*Urocitellus beldingi*) moved upslope in response to climate change during the past century, yet anthropogenic refugia, artificially supplementing food and water resources, facilitated population persistence along its low-altitude limit (Morelli et al., 2012). Another study found that porcupines (*Erethizon dorsatum*) had lower survival in the presence of a recolonizing carnivore (fisher), and this was exacerbated during severe winter weather (Pokallus & Pauli, 2015). Additionally, the recolonization or reintroduction of martens to historical locales indicates that a combination of factors, including climate, competition with sympatric carnivores, and prey availability forms their lower limit (Carlson et al., 2014; Manlick, Woodford, Zuckerberg, & Pauli, 2017; Zielinski, Tucker, & Rennie, 2017). One of the most interesting examples includes wolverines (*Gulo gulo*) in North America whose lower limit is positively associated with deep snowpack that is hypothesized to help preserve cached food and provide protection from competitors (Inman, Magoun, Persson, & Mattisson, 2012).

Other studies provide evidence that biotic factors alone can form lower limits. For example, shrub habitats were considered population sinks for Arctic ground squirrels (*Urocitellus parryii*) due to high predation rates (Donker & Krebs, 2012). This dynamic was also confirmed for arctic hares (*Lepus arcticus*) through a series of experiments (Barta et al., 1989; Small & Keith, 1992). There are also notable examples that indicate abiotic factors alone are the ultimate limits for low-latitude populations (Lenarz, Nelson, Schrage, & Edwards, 2009; Wattles, Zeller, & DeStefano, 2018). Similar to the examples provided previously, many of these studies could not identify the direct and indirect causal mechanisms that formed range limits.

1.5 Examples from other taxa and regions

There are numerous examples of taxa or mammals from other regions that support iRLT. We did not conduct a comprehensive review of these but present some to serve as starting points for future studies. There was support for iRLT along upper limits for European mammals (Acevedo, Jiménez-Valverde, Melo-Ferreira, Real, & Alves, 2012; Levänen, Kunnasranta, & Pohjoismäki, 2018; Taulman & Robbins, 1996), birds (Plummer, Siriwardena, Conway, Risely, & Toms, 2015), and plants (Hargreaves et al., 2014), and even bacteria (Simon et al., 2014). One study found that older-aged trees can facilitate survival and growth for seedling trees along high-altitude limits by providing shelter from harsh climate (Ettinger & HilleRisLambers, 2017). Other examples include the expansion of rats (*Rattus spp.*) (Varudkar & Ramakrishnan, 2015) and ticks (Leighton, Koffi, Pelcat, Lindsay, & Ogden, 2012) to high-latitude/altitude regions via indirect (rats) or direct (ticks) facilitation by humans.

We also found support for iRLT along lower limits for birds (Waite & Strickland, 2006), European mammals (Atmeh, Andruszkiewicz, & Zub, 2018; Levänen et al., 2018; Pedersen, Odden, & Pedersen, 2017), amphibians (Cunningham, Rissler, & Apodaca, 2009), and especially plants (Callaway et al., 2002; Hargreaves et al., 2014; Johansson et al., 2018; Loehle, 1998). For example, Canada jays (*Perisoreus canadensis*) rely on snow and cold weather to cache food for early breeding, yet warmer winters have exposed caches to rot and resulted in subsequent declines in reproduction (Derbyshire, Strickland, & Norris, 2015); ultimately this abiotic constraint could determine the low-latitude range limit for the species.

Overall, we found overwhelming support for abiotic and biotic factors impacting both limits of the range for the North American mammal studies that we reviewed. Although there was evidence for the classic predictions of RLT, much more evidence was found for the interactive effects predicted by our extension, iRLT.

1.6 Biotic interactions vary by trophic level

Our review provided insight on the biotic interactions that limit mammalian carnivore and herbivore populations along range edges. In accordance with RLT, biotic interactions were approximately three times as prevalent along lower limits (Table 1.4). We also found clear differences between carnivores and herbivores, providing support for trophic theory (Hairston & Hairston, 1993); competition was the only biotic interaction associated with carnivores (25 studies), whereas predation or parasitism was considered the limiting factor for 77% (55 of the 71 studies) of herbivore studies along range limits (Table 1.4). It is important to note, though, that many studies assume competition (Barrio, Hik, Bueno, & Cahill, 2013) when other biotic interactions might be structuring populations and communities. Also, there is known publication bias towards negative biotic interactions (Barrio et al., 2013), especially along lower edges (Cahill et al., 2014). The latter bias may have occurred for studies in our review. Even those that were not following RLT were likely predisposed to evaluate biotic interactions along lower limits given the prevalent assumption of this hypothesis in biogeography and ecology (Cahill et al., 2014).

Our findings highlight the different types of spatial patterns that biotic interactions can impart along range limits (Bull, 1991; Holt & Barfield, 2009) and provide insight into the underlying processes. Competition can create a variety of range-limit patterns (abrupt to diffuse) depending on phylogenetic and ecological similarity (Bull, 1991; Godsoe, Holland, et al., 2017; Wisz et al., 2013). For example, competition between highly similar carnivore species pairs (e.g., lynx-bobcats, red fox-arctic fox) is thought to create parapatric distributions (Hersteinsson & Macdonald, 1992; Peers et al., 2013). Species pairs that are still within the same taxonomic family but have contrasting body sizes (e.g., marten-fisher, red fox-coyotes) often have greater geographic and regional overlap (Jensen & Humphries, 2019; Krohn, Elowe, & Boone, 1995; Murray & Larivière, 2002). Contrastingly, near sympatry can occur for phylogenetically dissimilar species pairs with similar ecological associations (e.g., lynx-coyote; Guillaumet et al., 2015). There are notable exceptions (e.g., mesopredator release; Crooks & Soulé, 1999; Ritchie & Johnson, 2009), though, indicating that competition between similar species is not always the dominant biotic interaction that forms range limits for carnivores (see for example, Davis et al., 2018).

Comparatively, the patterns that predation and parasitism create along range limits are less well understood (Godsoe, Holland, et al., 2017). These biotic interactions can confer patterns similar to competition (e.g., parapatry) as shown by theoretical and empirical studies (e.g., apparent competition; Holt & Barfield, 2009; Poley et al., 2014). However, the mechanisms underlying predation and parasitism may also lead to divergent range patterns. In particular, the functional response of predators and parasites varies based on their degree of specialization and the density of prey and host populations (Holling, 1959). For example, snowshoe hares at lower latitudes, beyond the range of their specialist predator (lynx), often persist at low densities (Hodges, Mills, & Murphy, 2009; Linden et al., 2011). In regions where lynx are absent, generalist carnivores may exhibit a Type III functional response (density-dependent predation) (Chan et al., 2017; Todd, Keith, & Fischer, 1981) that potentially affords hares a low-density refuge from predation (Holt & Barfield, 2009; Oaten & Murdoch, 1975). Similarly, a low-density refuge may allow moose (*Alces alces*) to escape high parasite loads and explain their persistence in some regions along their low-latitude limit in North America (Samuel, 2007).

Low-density refuges occur in some aquatic ecosystems (Griffen & Williamson, 2008; Seitz, Lipcius, Hines, & Eggleston, 2001) and are akin to Janzen-Connell effects where plant seeds occurring at low density escape predation by seed (see review in Comita et al., 2014). We propose that Janzen-Connell effects, which describe predation patterns at local scales, may be extended to other trophic levels and at broader spatial scales. We suggest that a low-density refuge from predation provides a plausible explanation of why the ranges of some prey/host species extend further towards the equator than their carnivore/parasite counterparts. The extent to which this occurs, though, might be predicated on the quality and availability of unlinked biotic factors (e.g., habitat), which vary in space and time (e.g., Sinclair et al., 1998). The spatial pattern associated with our hypothesis might produce diffuse range margins compared to abrupt limits which are often associated with competition. As mentioned previously, there are other outcomes associated with predation or parasitism (e.g., apparent competition) that can lead to variable patterns along range limits (Bull, 1991; Holt & Barfield, 2009). However, few of these hypotheses have been tested experimentally or using empirical data.

1.7 Conclusions, limitations, and future directions

Our review indicates that the long-standing theory on range limits, proposed by Darwin (1859) and others since then, deserves to be broadened to include the interactive nature of abiotic and biotic factors along range margins. For populations along upper limits, abiotic factors will likely have more importance and directly influence range dynamics, whereas positive biotic factors have the potential to ameliorate harsh abiotic conditions. Conversely, biotic interactions will have greater importance along lower limits, but abiotic factors can mediate negative biotic interactions. For both scenarios of iRLT, the strength and direction of abiotic and biotic factors can be used to predict range expansion, contraction, or stability.

iRLT has properties comparable to the stress-gradient hypothesis (SGH) and condition-specific competition (CSC) (Table 1.1). It is most similar to the SGH, yet this hypothesis has only recently been advocated for understanding animal distributions (Barrio et al., 2013) with only a few tests (e.g, Peoples et al., 2015). However, SGH focuses solely on biotic interactions which may be an incomplete model for mobile animals that are influenced by unlinked biotic factors (e.g., habitat or prey availability) and biotic interactions (Jensen & Humphries, 2019). Similar to the SGH, iRLT provides a conceptual framework to evaluate positive biotic factors which is important as the inclusion of these are lacking in range-limit studies, especially for animals (Barrio et al., 2013). However, SGH does not predict interactions between abiotic and biotic factors along lower limits. As shown below, CSC is more similar to iRLT in this regard.

Like iRLT, CSC provides a framework to evaluate asymmetric competition through the lens of environmental gradients. The premise of CSC is that interacting species will either gain or lose competitive advantage based on the environmental conditions. For example, Taniguchi et al. (2000) found that salmonids adapted to colder conditions performed better than closely related species but performed poorly when temperatures were higher. Although CSC is focused on animals (Connell, 1961; Nagamitsu et al., 2010), it has not been applied to mammals. Our review indicates that CSC is applicable to mammals. For example, abiotic factors associated with winter (e.g., snow, cold temperature) were often positively correlated with the distribution of boreal carnivores along lower limits; in these cases, harsh climate was thought to mediate competitive interactions with more temperate species (Dekker, 1989; Jensen & Humphries, 2019; Krohn et al., 1995; Peers et al., 2013). However, unlike CSC, iRLT includes other biotic interactions such as predation, parasitism, and facilitation, which can lead to a variety of range-limit patterns. Indeed, snow or cold temperatures can have a strong positive effect on boreal herbivores, buffering predation (Bastille-Rousseau et al., 2018; Zimova et al., 2016) and parasitism (Bowman et al., 2005; Murray et al., 2006).

Interactive models of range limits such as ours, CSC, and the SGH may require a different inferential framework to understand *causes* of range limits. Most studies in our review were correlative and did not evaluate fitness (e.g., growth rates) along range limits. Modeling frameworks that allow for the inclusion of correlated direct and indirect predictors, like structural equation modeling (Joseph, Preston, & Johnson, 2016), provide a promising avenue (see for example Duclos et al., 2019). Future research could prioritize large-scale observational studies that collect data on direct and indirect effects at the same spatial and temporal scale, as well as extend beyond the range of the focal species to identify limiting factors (Louthan et al., 2015; Westoby et al., 2017). This type of experimental design is well suited for evaluating direct and indirect effects using a causal modeling framework (Joseph et al., 2016). Ideally, though, large-scale studies should be supplemented with lab experiments (e.g., Malenke et al., 2011) to determine how gradients of abiotic stress and biotic factors influence population growth rates and thus range limits (Godsoe, Jankowski, et al., 2017; Louthan et al., 2015).

We consider iRLT to be applicable to different taxa and regions and encourage researchers to think critically of the biotic interactions and factors that limit each trophic level. Competition appears to be a limiting factor for plants and carnivores along lower margins (Hargreaves et al., 2014; Peers et al., 2013), whereas predation/parasitism likely regulates herbivores (Anderson et al., 2009; Murray et al., 2006). Regardless of these differences, the predictions of iRLT remain similar. However, the types of biotic interactions, which vary by trophic level, may create different patterns along range limits and result in differences in range contraction, expansion, and stability. Our examples using snowshoe hares and moose provide a starting point to explore the interactive nature across trophic levels. Specifically, the lower limits of herbivores, which (like carnivores) appear to be influenced by climate-mediated biotic interactions, may contract at different rates and lag those of their carnivore counterparts. This may be a particularly interesting avenue of research to explore considering climate change predictions.

Our review does not incorporate many intraspecific factors or evolutionary considerations (e.g., dispersal ability, Allee effects) which could greatly influence range limits (Parmesan, 2006; Sexton et al., 2009). However, there are numerous examples that indicate iRLT is relevant for understanding the influence of these factors on range limits. For instance, phenotypic and/or genotypic variability may rescue populations along lower limits; either of which can occur naturally or from facilitation by humans (Atmeh et al., 2018; Jones et al., 2018; Mills et al., 2018). Furthermore, population size can ameliorate the influence of harsh climate along range limits and influence the rate of expansion (Grayson & Johnson, 2018). There are other eco-evolutionary dynamics such as within-species trait differences associated with dispersal along upper range limits (Hughes, Dytham, & Hill, 2007; Simmons & Thomas, 2004).

Identifying abiotic and biotic mechanisms that limit ranges is critical for predicting future distributions and developing appropriate conservation and management strategies. This is especially important considering current and anticipated threats from climate change, habitat loss, and species invasions (Mantyka-Pringle, Martin, & Rhodes, 2012). iRLT can improve predictions of species responses to global change and thus lead to better decision making. We encourage future research to explore the interactive nature of abiotic and biotic factors to better understand why range limits form and change over time.

Table 1.1 Summary of hypotheses and models on the causes of range limits.

Hypothesis/Model	Category	Premise of hypothesis/model	Relevant taxa	Notable papers
Species Distribution Models/Environmental Niche Models/Climate Envelope Models	Abiotic	These models assume that animals and plants track a climate niche, i.e., their distributions are their fundamental niche. These models are perhaps the most common approaches for evaluating species distributions.	Plants and animals	Pearson and Dawson (2003), Soberón (2007)
Climatic Variability Hypothesis	Abiotic	This hypothesis posits that species are more temperature-limited in aseasonal environments and have narrow temperature niches than species living in seasonal and harsher climates, which explains narrower altitudinal distributions in tropical areas.	Plants and animals	Janzen (1967); Ghalambor et al. (2006)
Abundant-centre model/Abundant center hypothesis/Central margin hypothesis/Centre-periphery hypothesis	Biotic	These hypotheses and models predict that abundance, fitness, or genetic diversity is highest at the center of a species geographic range and declines towards each edge.	Plants and animals	Brown (1984); Gaston et al. (2000); Carter and Prince (1981); Pironon et al. (2017)
Asymmetric Abiotic Stress Limitation Hypothesis (AASL); Species Interactions-Abiotic Stress Hypothesis (SIASH); Stress-tradeoff hypothesis (STH)	Abiotic or biotic	These contributions are all centered around the classic hypothesis described by Darwin (1859), Connell (1961), Dobzhansky (1950), and MacArthur (1984), which posits that abiotic factors form high-latitude/altitude limits and biotic interactions form lower limits.	Plants and animals	Darwin (1859); Dobzhansky (1950); Connell (1961); MacArthur (1984); Normand et al. (2009); Louthan et al. (2015); Anderegg and HilleRisLambers (2019)
Stress-gradient hypothesis (SGH)	Interactive	This hypothesis postulates that gradients of environmental stress determine the extent to which competition affects populations. Those living along lower edges, in less stressful environments, are more likely to experience competition, whereas those along upper edges, where abiotic stress is thought to be higher, are more likely to experience positive biotic interactions (e.g., facilitation).	Plants	Callaway et al. (2002); Ettinger and HilleRisLambers (2017)
Condition-Specific Competition (CSC); Resource Availability Hypothesis	Interactive	The main premise of this hypothesis is that interacting species will either gain or lose competitive advantage based on environmental conditions and this will in turn affect their distributions.	Animals	Connell (1961); Taniguchi et al. (2000); Malenke et al. (2011); Srinivasan et al. (2018)

Table 1.2 Outline of predictions for range-limit theory (RLT) and interactive range-limit theory (iRLT).

Predictions of factors causing range limits

	High-latitude/altitude limit	*Low-latitude/altitude limit*
RLT	Negative abiotic factors	Negative biotic interactions
iRLT	Negative abiotic factors AND Positive biotic factors	Negative biotic interactions AND Positive abiotic factors

Predictions for contraction along range limits

	High-latitude/altitude limit	*Low-latitude/altitude limit*
RLT	Negative abiotic factors increase	Negative biotic interactions increase
iRLT	Negative abiotic factors increase AND/OR Positive biotic factors decrease	Negative biotic interactions increase AND/OR Positive abiotic factors decrease

Predictions for expansion along range limits

	High-latitude/altitude limit	*Low-latitude/altitude limit*
RLT	Negative abiotic factors decrease	Negative biotic interactions decrease
iRLT	Negative abiotic factors reduce AND/OR Positive biotic factors increase	Negative biotic interactions reduce AND/OR Positive abiotic factors increase

Table 1.3 Number of studies that found positive, negative, and neutral effects of abiotic and biotic factors on range limits of North American mammals. Note: This table only includes studies that evaluated both abiotic and biotic factors along range limits (n = 138).

Range-limit	Factor	Positive	Negative	Neutral	Biotic interaction[a]	Total[b]
High	Abiotic	13	61	1		75
	Biotic	57	18	7	3	85
Low	Abiotic	46	15	11		72
	Biotic	49	12	4	9	74

[a] Few studies coincidentally evaluated biotic interactions (e.g., competition, predation) at broader spatial scales.

[b] Note that some studies documented multiple abiotic or biotic factors, which occasionally had opposite signs. For example, if a study indicated that one abiotic variable had a positive effect, and another had a strong negative effect, we tallied these as separate records, which increased the total number of studies.

Table 1.4 Number of biotic interactions by trophic level and range-limit position reported by 92 of 290 studies (32%) included in the integrative review.

Trophic Level	Range-Limit	Competition	Predation/Parasitism
Carnivore	High	6	0
	Low	19	0
Herbivore	High	6	18
	Low	10	37

Figure 1.1 Range-limit theory (RLT) a) predicts that abiotic factors (blue) constrain the high-latitude/altitude (upper) limit of the potential range (gray dashed lines) and biotic interactions (green) constrain the low-latitude/altitude (lower) edge of the potential range, resulting in the black outlined observed range. Interactive range-limit theory (iRLT) b) extends RLT to predict that the interaction of abiotic and biotic factors forms limits at either edge of a range. Positive biotic factors can expand the range along upper limits despite negative abiotic factors, and expansion along lower edges can result if negative biotic interactions are ameliorated by stress from abiotic factors. RLT posits that c) species like bobcat (*Lynx rufus*, bottom) are limited by abiotic factors (e.g., climate) on the upper edge, and e) those such as Canada lynx (*Lynx canadensis*) are limited by biotic interactions (e.g., competition for prey) along the lower limit. iRLT predicts that d) positive biotic factors (more prey for bobcats) can ameliorate negative abiotic factors along high-latitude/altitude limits and f) positive abiotic factors (increase in snow for lynx) mediate negative biotic interactions along lower limits.

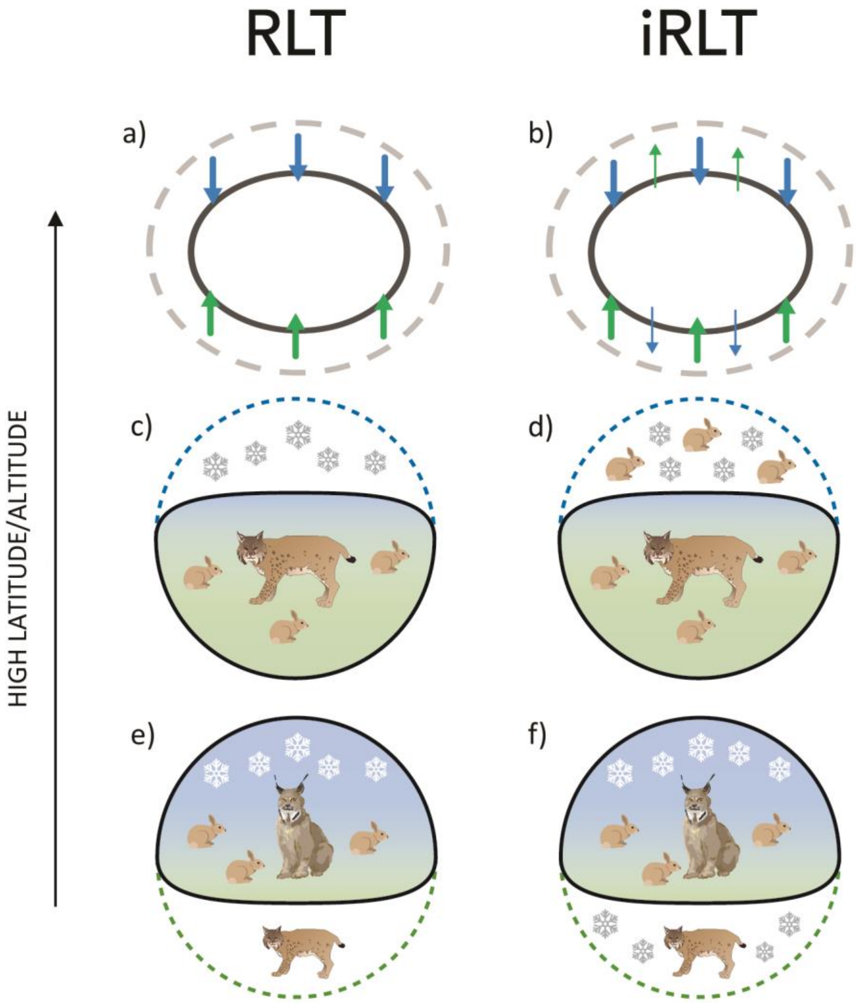
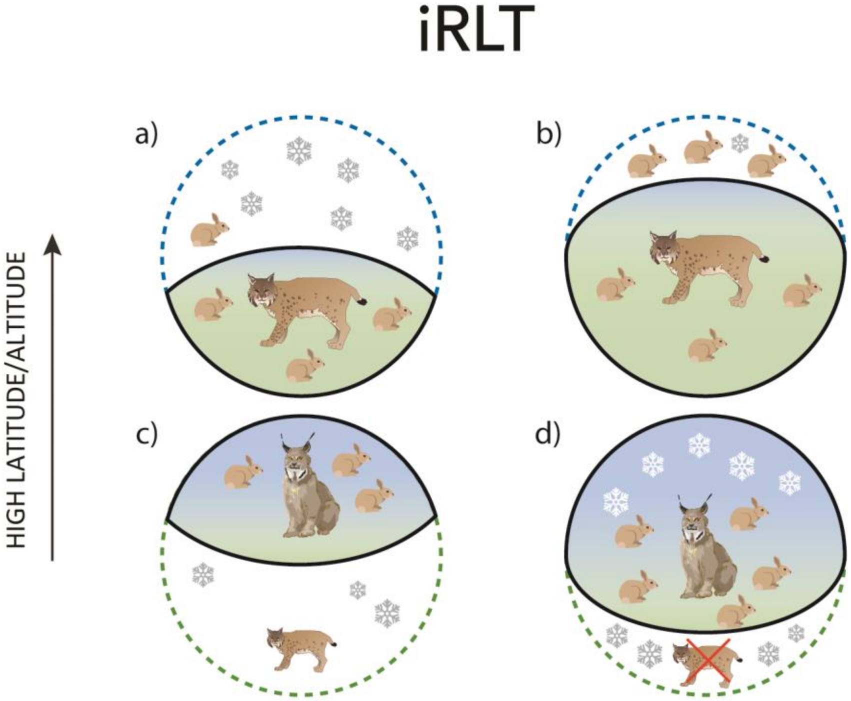


Figure 1.2 Interactive range-limit theory (iRLT) provides predictions for expansion and contraction along each edge. For high-latitude/altitude limits, a) range contraction (e.g., of bobcat) occurs when abiotic stress is greater (increased snow) than the influence of positive biotic factors and b) range expansion occurs when positive biotic factors (e.g., more prey) are greater than abiotic stress. For low-latitude/altitude limits, c) range contraction (e.g., of lynx) occurs when negative biotic interactions (increased competition) are greater than the influence of abiotic factors d) and expansion occurs when this dynamic is reversed. In summary, positive biotic factors can expand the range along upper limits despite the presence of stressful abiotic factors, and expansion along lower limits can result if negative biotic interactions are buffered by stress from abiotic factors; contraction occurs in the absence of these indirect and mediating factors along either edge.



CHAPTER 2

ABIOTIC STRESS AND BIOTIC FACTORS MEDIATE RANGE DYNAMICS ON OPPOSING EDGES: A TEST OF INTERACTIVE RANGE-LIMIT THEORY (IRLT)

2.1 Introduction

The causes of range limits have long fascinated biogeographers and ecologists. An enduring theory postulates that harsh climate forms upper latitudinal/altitudinal boundaries and biotic interactions form lower limits (Connell, 1961; Darwin, 1859; Dobzhansky, 1950; MacArthur, 1984). Despite its widespread acceptance, there is mixed support for this idea (Louthan et al., 2015; Normand et al., 2009) or for others that only evaluate the influence of abiotic factors (e.g., environmental niche models) or biotic processes (e.g., abundant-center hypothesis) on range limits (Sexton et al., 2009). This lack of clarity, combined with the observed and predicted impacts of climate change, has spurred an interest in developing a unified theory on range-limits (Connallon & Sgrò, 2018; Sirén & Morelli, 2019).

A new contribution – interactive Range-Limit Theory (iRLT) – highlights how the interplay between abiotic and biotic factors forms limits and causes shifts in a species' range (Sirén & Morelli, 2019). Positive biotic factors, such as prey or habitat availability, can ameliorate abiotic stress along upper limits. Conversely, abiotic stress can mediate negative biotic interactions (e.g., competition or parasitism) for populations along lower limits. These positive abiotic and biotic effects can interact with direct limiting factors to form range boundaries and facilitate shifts. Thus, iRLT provides a framework to evaluate how the interactions between abiotic and biotic factors form range limits and how this varies by upper and lower distributional edges.

As is common with bioclimatic transition zones (Risser 1993), the boreal-temperate ecotone of eastern North America includes the range limits of many species, including several winter-adapted and temperate mammalian carnivores (Kays, Gompper, & Ray, 2008; Ray, 2010). As such, they present an excellent opportunity to evaluate iRLT (Sirén & Morelli, 2019) and the impacts of climate change on ecological communities (Goldblum & Rigg, 2010). Prior research within this ecotone indicates that carnivore populations along upper latitudinal/altitudinal limits, such as bobcats (*Lynx rufus*) and fisher (*Pekania pennanti*), are constrained by deep snow and cold temperatures, whereas those along lower limits (e.g., Canada lynx [*Lynx canadensis*], American marten [*Martes americana*]) are limited by competition or lack of prey and suitable habitat (Carlson et al., 2014; Jensen & Humphries, 2019; Peers et al., 2013; Peers, Wehtje, Thornton, & Murray, 2014). In accordance with iRLT, though, abundant prey and harsh winters can mitigate the negative effects for populations along upper and lower limits, respectively (Sirén & Morelli, 2019).

Here, we empirically test the hypotheses and predictions set forth by iRLT using data from a suite of carnivores at their latitudinal or altitudinal range limits, in the boreal-temperate ecotone in the northeastern United States: the upper limit of bobcats, coyotes (*Canis latrans*), and fishers, and the lower limit of lynx and marten (Hoving et al., 2005; Jensen & Humphries, 2019; Reed et al., 2017). It is unclear which mechanisms drive distribution dynamics of these species, including the extent to which climate, competition, and prey availability influence range limits. We propose that the lack of clarity is due to the correlative nature of these factors and how they interact to indirectly or directly influence populations along lower and upper edges. Disentangling these correlated effects will be necessary to more accurately predict, and ultimately prepare for, climate change responses along range edges.

We evaluated the hypotheses of iRLT using remote-camera data collected over a 6-year period (2014–2019) to understand how abiotic and biotic factors influence carnivore populations along range edges. Our first hypothesis was that snow has a direct limiting effect on populations along upper edges but that unlinked biotic factors (i.e., denisty-independent, Anderson 2017), such as prey or habitat availability, ameliorate harsh conditions and indirectly form range limits (Table 2.1, Fig. 2.1). Accordingly, we predicted that snow would have a negative and direct effect for carnivore populations along upper edges, whereas increased prey and habitat availability would have positive direct and indirect effects, respectively (Table 2.2, Fig. 2.1). For populations along lower limits, we hypothesized that snow mediates competitive interactions between phylogenetically and ecologically similar species and ultimately affects range limits (Table 2.1, Fig. 2.1). Following this idea, we predicted that snow would have a positive and indirect effect and mediate competitive interactions for carnivore populations along lower edges (Table 2.2, Fig. 2.1).

2.2 Materials and Methods

2.2.1 Study area

Our study area was located in the northeastern U.S. within the states of New Hampshire and Vermont (Fig. 2.2). This region is part of the transition zone between northern hardwoods and boreal forests, and includes wildlife and vegetative communities unique to eastern North America (Goldblum & Rigg, 2010). Elevation within the study area ranged from the lowest valleys at 3 m to the highest peaks in the region at 1,487 m and latitude ranged between 42.8–45.3°N. Boreal forest was generally found at higher elevation throughout the region and low elevation in the north.

The climate of the region is humid with mild and rainy summers and cold winters with deep snow (Davis et al., 2013). Annual precipitation varies between 101–160 cm and snowfall ranges from 244–406 cm, with deeper snow at high elevation and northern regions (Davis et al., 2013; USDA, 2007). July is the warmest month averaging 18°C (11°C to 27°C) and January the coldest month averaging -11°C (-15°C to -2°C; USDA 2007).

2.2.2 Data collection

We used data from 257 camera-trap sites operating from 9 January 2014–12 July 2019. Cameras were spaced in non-overlapping grids based on the home range size of the smallest carnivore species (marten = 2x2 km; Sirén, Pekins, et al., 2016; Sivy et al., 2017; Fig. 2.2) and set to take 1–3 consecutive pictures every 1–10 sec when triggered, depending on the brand and model. Each site included a remote camera positioned facing north on a tree, 1–2 m above the snow surface, and pointed at a slight downward angle towards a stake positioned 3–5 m from the camera (Fig. 2.2, inset). A GPS unit (Garmin GPS 62/64s, Garmin International, Olathe, KS, USA) was used to mark the location of each site when position error was <10 m. Commercial skunk (*Mephitis mephitis*) lure and wild turkey (*Meleagris gallopavo*) feathers were used as attractants and placed directly on the snow stakes. Cameras were checked on average 3 (range = 1–9) times each year to download data, refresh attractants, and to ensure cameras were working properly. For more information on the camera method see Sirén et al. (2018).

2.2.3 Statistical methods

2.2.3.1 Approach

We took a two-step modeling approach to evaluate our hypotheses. First, we used detection/non-detection data of carnivore and prey species (see Table 2.2) from camera surveys to run single-season occupancy models to derive the best unbiased estimates of occurrence. We then included these estimates as response and predictor variables within a structural equation modeling (SEM) framework to evaluate hypotheses of iRLT. For an overview of SEM, see Text A1 in Appendix B.

2.2.3.2 Single-season occupancy models

To generate species occurrence data for SEMs, we used camera data from 16 October–15 May (2014–2019) that was based on species' ecological responses to snowpack and leaf phenology of the region (Sirén, Maynard, Kilborn, & Pekins, 2016; Vashon et al., 2008) and approximates demographic (i.e., births and deaths) and geographic closure (i.e., dispersal) for the focal carnivores. Thus, we assumed that any violations of closure would be random and negligible due to limited temporal overlap with births and dispersal and our broad spatial sampling. We organized camera data into weekly occasions using CPW Photo Warehouse (Ivan & Newkirk, 2016) and recorded whether or not each species was detected during the occasion. We analyzed these data using a single-species, single-season occupancy model (MacKenzie et al., 2017) to estimate detection probability (ρ) and generate estimates of site-specific occupancy probabilities for each carnivore and prey species (Table 2.2). Several camera sites were either collocated or moved within the same grid during the study; we collapsed these data as we considered sites within the same grids as non-independent sampling units. Because we used data from multiple years, we used a ‘stacked’ design that included the year of sampling as a fixed effect for detection and occupancy probability. All occupancy analyses were performed in R (R Core Team, 2019) using the ‘unmarked’ package (Fiske & Chandler, 2011).

We used a combination of observational and site covariates (Table 2.1) to evaluate detection probability for each carnivore and prey species (Table 2.2). Specifically, we modeled detection probability as a function of temperature (°C), snow depth (cm), site-level biomass of vegetation (metric tons/ha), number of weeks since a camera was checked, and the week of each survey year. We fit a second-order polynomial for week as we expected a non-linear relationship between detection probability and time for most species. We used PRISM data for temperature (Daly et al., 2008) and SNODAS data for snow depth (Barrett, 2003); both products provide daily predictions at the 4 km (PRISM) and 1 km (SNODAS) spatial resolution. Forest biomass data was created using a 30 m resolution dataset of forest succession and disturbance that covered the northeastern U.S. (McGarigal, Compton, Plunkett, DeLuca, & Grand, 2017b). Prior to modeling we screened all detection covariates for multicollinearity using Pearson’s correlation (r) and variance inflation factors (VIF); detection covariates were all weakly correlated (r <0.5) and had VIF scores <2, so we allowed all combinations in models.

To maximally explain detection and thus provide the most unbiased estimates of occupancy, we evaluated all possible combinations of detection covariates, resulting in a total of 48 models, while fitting a global occupancy model which we held constant. We evaluated model performance using Akaike Information Criterion (AIC) scores and chose the most parsimonious model within 2 AIC units of the top model (Burnham & Anderson, 2002). Finally, to determine how well the models fit the data and to evaluate assumptions of closure, we conducted goodness-of-fit tests using the ‘parboot’ function in the ‘unmarked’ package, running 500 bootstrapped iterations of the top detection model for each species. We considered models to fit the data if the summed square of residuals (SSE) of the top models were within the distribution of the bootstrapped SSE (Kéry & Royle, 2015).

2.2.3.3 Structural Equation Models (SEM)

To evaluate the direct and indirect effects of abiotic and biotic factors on upper and lower range limits, we used a SEM framework that is useful for disentangling correlated variables to identify causal relationships (Grace, 2008). For an overview of SEM, see Text A1 in Appendix B. To create exogenous predictor data for the SEM analysis, we calculated average values of abiotic and biotic factors from each camera site and point estimates of occupancy for each species. We specified snow duration (days), mean and maximum snow depth (cm) and forest biomass (metric tons/ha) as exogenous variables in SEMs (Table 2.1, Fig. 2.1), using SNODAS (Barrett, 2003) and forest succession and disturbance (McGarigal et al., 2017b) data, respectively. Forests with lower biomass values were considered early-successional forest, whereas those with higher values were late-successional (McGarigal et al., 2017b). We smoothed the snowpack and biomass layers using a Gaussian kernel function with a custom bandwidth that was relevant to the scale of our sampling (4 km^2 grids) and extracted smoothed values from the camera survey locations using the ‘extract’ function in the ‘raster’ package (Hijmans et al., 2015).

For each species, we extracted the empirical best unbiased predictor (BUP) of occupancy from camera survey locations during each year they were operational using the ‘ranef’ and ‘bup’ functions in ‘unmarked’ (Fiske & Chandler, 2011). We extracted BUPs from occupancy models that only included top detection covariates; ‘Year’ was included as a fixed effect on detection and occupancy to account for our stacked design. Abiotic and biotic occupancy predictors were excluded to avoid any potential confounding from using the same occupancy covariates in the SEM (e.g., snow duration). Instead, we maximally explained detection and derived conditional (on data and on predicted site-specific detectability) estimates of occupancy. We then used these corrected estimates of occurrence as response and predictor variables in SEMs to explore causal drivers of species’ occurrence patterns. We used the BUPs from each prey species to create prey availability predictor/response variables for the SEMs by summing across species within the same range-limit group (see Table 2.2 and Fig. 2.1 for a complete description).

Using snow and biomass as exogenous variables and derived estimates of occupancy (i.e., BUPs) as response and predictor variables, we employed d-sep tests (Lefcheck, 2016; Shipley, 2009) to identify direct and indirect effects. We fit a series of univariate generalized linear mixed-effects models (binomial distribution with logit-link function) in each SEM using the ‘lme4’ package (Bates, Maechler, Bolker, & Walker, 2015); for all models, ‘camera’ was specified as a random effect due to repeated measurements and variability in effort across years. For variables whose causal relationships were either unknown or implausible, we fixed their error terms as free covariances (Fig. 2.1). We assessed d-sep of each SEM by evaluating the Pearson’s χ^2 statistic of a Fisher’s *C* test, where a $P > 0.05$ indicates adequate fit of the observed data and conditional independence (Shipley, 2009). If a SEM was d-sep (i.e., conditionally independent), the path coefficients (i.e., relationships between nodes) from the univariate regressions were used to calculate direct and indirect effects. Direct effects were considered as connected nodes and indirect effects were considered as those separated by one node; path coefficients of indirect effects were the product of two direct path coefficients (Fig. 2.1). Path coefficients were considered significant if their 95% confidence intervals did not overlap zero; indirect effects were only significant if both individual connecting paths were significant. We also reported the conditional R^2 values for each species, which explain the proportion of variance explained by the fixed and random effects. We used the ‘piecewiseSEM’ package in R (Lefcheck, 2016) to perform d-sep tests and evaluate SEMs. In summary, we evaluated 3 global SEMs each containing a different exogenous snowpack variable (mean snow depth, maximum snow depth, and mean snow duration) while holding other variables constant (Table 2.1, Fig. 2.1).

2.3 Results

2.3.1 Single-season occupancy models

The top-performing detection models included a number of covariates that explained detection probability of carnivore and prey species (Tables A1–A2, Figs. A3-

A2 in Appendix B); these covariates were held constant (along with ‘Year’ fit on ρ and ψ) to generate species-specific occupancy estimates for SEMs. For most species, the summed square of residuals (SSE) of the top models were well within the distribution of the bootstrapped SSEs, indicating they fit the data well (Table A3 in Appendix B). There was evidence for a lack of fit for snowshoe hares (*Lepus americanus*) that had a significantly higher SSE ($P = 0.006$; Table A3 in Appendix B) than bootstrapped SSEs, indicating overdispersion. This may have occurred due to variance in occupancy across years, potentially because hare populations can fluctuate annually (Keith, Bloomer, & Willebrand, 1993). As hares are an important food source for several carnivores (Litvaitis & Harrison, 1989; Simons-Legaard et al., 2016), we retained it as a prey species in its respective group (Table 2.2).

2.3.2 Structural equation models (SEM)

We evaluated three global SEMs that represented hypotheses of iRLT and alternative hypotheses on range limits using a piecewise approach. Of these SEMs, two fit the data well (snow duration: Fisher’s C = 7.906, $P = 0.245$; snow depth: Fisher’s C = 8.664, $P = 0.193$), indicating d-separation (i.e., conditional separation). For brevity, we only report results from the snow depth SEM because inference was similar between SEMs. The snow depth SEM explained 15%–53% of the variation in carnivore occurrence and 1%–10% of the variation in prey occurrence (Figs. 2.3–2.4, Figs. A3–A4 in Appendix B). Although we included the red fox (*Vulpes vulpes*) in the SEMs, this species did not impart strong effects on other species, nor was it influenced by others.

2.3.2.1 Direct and indirect causes of upper limits

Snow depth had a direct negative effect on bobcat and coyote occupancy along upper limits (Table 2.3, Fig. 2.3, Fig. A3 in Appendix B). However, prey availability along upper limits (deer [*Odocoileus virginianus*], turkey, porcupines [Erithizon dorsatum], gray squirrel [*Sciurus carolinensis*]) and lower limits (snowshoe hare, red squirrel [*Tamiasciurus hudsonicus*], grouse [*Bonasa umbellus*], moose [*Alces alces*]) had an equally strong direct effect on bobcats (Fig. 2.3), whereas prey availability along upper limits had a stronger direct effect than snow for coyotes (Fig. A3 in Appendix B). Snow depth also had an indirect negative effect on these species due to its negative influence on prey along upper edges (Fig. 2.3, Fig. A3 in Appendix B). This was countered, especially for bobcats, by a positive direct effect on prey availability along lower limits (Fig. 2.3). Snow also had a direct negative effect on fisher along their upper limits (Table 2.3, Fig. A4 in Appendix B). However, we did not find any direct effects of prey or indirect effect of habitat through prey on this species. Forest biomass had an indirect effect on bobcat and coyote occupancy, specifically through its direct effect on prey availability (Fig. 2.3, Fig. A3 in Appendix B).

2.3.2.2 Direct and indirect causes of lower limits

Snow depth and prey availability along lower limits had a direct and positive influence on lynx occupancy (Table 2.3, Fig. 2.3). However, we found that the direct negative effect that snow depth had on bobcats produced a stronger indirect positive effect on lynx by mediating the direct negative effect that bobcats have on lynx occupancy (snow → bobcat → lynx; Table 2.3, Fig. 2.3). Coyotes had the strongest direct effect on lynx (Fig. A3 in Appendix B), but the indirect effect of snow through coyotes (i.e., snow → coyote → lynx) was considerably less than bobcats. These effects were evident for fisher on lynx but less so compared to bobcats and coyotes (Table 2.3, Fig. A4 in Appendix B). A similar but less prominent indirect effect of snow on lynx occupancy also occurred via prey availability along lower limits (snow → prey availability → lynx; Fig. 2.3). An indirect effect of forest biomass on lynx occupancy also occurred through prey availability (biomass → prey availability → lynx; Fig. 2.3). However, we did not detect any direct effect of forest biomass on lynx occupancy (Fig. 2.3).

Snow depth also had a direct positive effect on marten occupancy as did forest biomass and prey availability on lower limits (Fig. 2.4). Coyotes were the only species that had a direct negative effect on marten occupancy (Table 2.3, Fig. 2.4). Although less prominent, we also detected a positive indirect effect of snow depth on marten occupancy through a direct negative effect from coyotes (Table 2.3; Fig. 2.4), indicating that snow mediated interactions between these species. Like lynx, forest biomass also had an indirect effect on marten occupancy through prey availability along lower limits, whereas, unlike lynx, forest biomass also imparted a strong direct effect on marten occupancy (Fig. 2.4).

2.4 Discussion

Although many past studies assume that biotic interactions limit species along lower latitudinal/altitudinal edges, support for this hypothesis is equivocal (Cahill et al., 2014). Further, few studies have given credence to the potential for positive biotic factors to ameliorate harsh climate along upper limits (but see Ettinger & HilleRisLambers, 2017). Our study is one of the first to utilize a causal framework to identify causes of range limits. As such, we were able to disentangle many correlated abiotic and biotic factors and shed light on previous work.

We found strong support for our hypothesis that snow directly limits populations along upper edges, but that prey and habitat availability have strong direct and indirect positive effects, respectively. As predicted, snow had a direct and negative effect on bobcats, coyotes, and fishers. Prior studies have found these species to have a negative association with deep snow (Dowd, Gese, & Aubry, 2014; Krohn et al., 1995; Reed et al., 2017; Scully et al., 2018; Zielinski et al., 2017), likely due to limited mobility that can contribute to starvation (Bekoff & Wells, 1981; Litvaitis, Clark, & Hunt, 1986; McCord, 1974). However, the availability of all prey species (i.e., those upper and lower limits) countered the negative effect of snow for bobcats and coyotes, indicating the importance of food in areas with harsh climate. Indeed, the reliance on a diversity of prey, and larger prey species in particular, is important for bobcats and coyotes during winter in the northern part of their range (Litvaitis & Harrison, 1989; Litvaitis et al., 1986; Litvaitis, Stevens, & Mautz, 1984; Newbury & Hodges, 2018).

The indirect effects of snow and forested habitat on bobcats and coyotes via their association with prey is worth noting. It seems that bobcats benefit from either mild or harsh winters because of the differential effect that snow has on prey along upper or lower limits. Indeed, northern bobcats have a plastic diet that varies by winter severity (Litvaitis et al., 1986; Newbury & Hodges, 2018). Further, we found that low biomass forest (a proxy for early-successional forest) has a direct positive effect for prey along upper and lower limits that in turn benefits bobcats and coyotes along their upper limits. This dynamic was attributed to the northward expansion of bobcats in New England during the 1900s when much of the region was early-successional forest, yet winters were still considered severe (Litvaitis et al., 2006). A similar bottom-up process is thought to allow fisher to persist in deep snow regions (Jensen & Humphries, 2019; McLellan et al., 2018). Although harsh climate has a negative and direct effect on species along upper limits, the direct benefits of available prey mediated by climate and habitat can play an equal role.

Our study highlights the negative effect that competitors have on populations along lower limits, consistent with the long-standing hypothesis that biotic interactions are more influential along lower range boundaries (Louthan et al., 2015). However, our results also indicate strong support for iRLT. For example, snow had a strong positive effect on lynx and marten occupancy along their lower limits. These results are consistent with other studies (Hoving et al., 2005; Krohn et al., 1995). However, there was stronger evidence of an indirect effect for lynx; snow depth mediated occupancy of bobcats, its primary competitor, that had a negative effect on lynx occupancy. There was also evidence for a positive, indirect effect of snow on martens through a direct negative effect of snow on coyotes. This was less prominent than the bobcat-lynx relationship but is aligned with our hypothesis of how climate mediates competition along lower limits and also explains the positive association with snow commonly identified by other studies (Sirén & Morelli, 2019).

We were surprised by the strong negative effect that coyotes had on martens. Although martens are known to be preyed upon by coyotes (Sirén, 2013), more common predators include red fox and fishers (Hodgman, Harrison, Phillips, & Elowe, 1997; Nicholas P. McCann, Zollner, & Gilbert, 2010; Thompson, 1994). We hypothesized that fishers would be the primary competitor as they are phylogenetically similar and previous correlative work provides evidence of competitive interactions (Jensen & Humphries, 2019; Krohn et al., 1995; Manlick et al., 2017). It is plausible that the strong negative effect that coyotes had on martens represents a cascading effect that coyotes have on the rest of the carnivore community (Jensen & Humphries, 2019). Additionally, the resolution of occupancy data might be too coarse and preclude a nuanced understanding of competitive interactions between species (Jensen & Humphries, 2019). Clearly, more community-level demographic studies are needed to differentiate the true competitors from the indirect ones.

The stronger direct effect of snow on martens, compared to lynx, suggests that this abiotic factor provides other benefits, such as subnivean habitat for foraging or resting (Buskirk, Forrest, Raphael, & Harlow, 1989; Spencer, 1987). Similarly, lynx directly benefit from snow in several ways, including thermoregulation and differential hunting success (Kolbe & Squires, 2007; Stenseth et al., 2004). There was a notable indirect effect that habitat availability had on lynx through associated prey species (hare, red squirrels, moose, grouse). Indeed, this effect, like that of bobcats, was associated with low biomass forest (early-successional forest) because preferred prey was more available in these habitats as shown in other studies (Litvaitis, Sherburne, & Bissonette, 1985; McCann & Moen, 2011). Finally, biomass had a strong positive direct and indirect effect on marten, likely because forests with high biomass are important for protection from predators and provide foraging and denning opportunities (Hodgman, Harrison, Katnik, & Elowe, 1994). Collectively, these findings indicate that several factors cause lower range limits and likely expansion.

By using a causal framework we were able to show that abiotic factors can mask biotic interactions due to strong intercorrelations. The effect of these intercorrelations has been demonstrated through simulation (Godsoe, Franklin, et al., 2017) and cited as a reason why many past studies might have failed to detect the role of biotic interactions along lower range limits (Sexton et al., 2009; Sirén & Morelli, 2019). For example, modeling lynx occurrence as a function of snow depth and bobcat occurrence using a traditional correlative framework would have presented problems due to multicollinearity. This issue was resolved using SEM which allows for the inclusion of correlated predictors to identify direct and indirect effects (Grace, 2008). Besides adopting a causal framework, we also collected large scale data on biotic interactors (i.e., competitors and prey) and sampled beyond the range limit of several focal species. Both of these approaches have been advocated by previous work (Westoby et al., 2017; Wisz et al., 2013). As such, we were able to show that abiotic stress mediates competition along lower range limits and that positive biotic factors can ameliorate harsh climate along upper limits.

From a conservation perspective, we found that a combination of competitors limit lynx along their southern range limit. In particular, coyotes, bobcats, and, recently, fisher are considered the primary threat to lynx populations in the conterminous U.S. (Bayne, Boutin, & Moses, 2008; Bunnell, Flinders, & Wolfe, 2006; McLellan et al., 2018; Peers et al., 2013). Our study supports these findings. However, we found bobcats to have the greatest impact on lynx occupancy through the indirect effect of snow and competition for similar prey. Bobcats and lynx are closely related and can hybridize (Koen, Bowman, Lalor, & Wilson, 2014; Schwartz et al., 2004); thus, competition between these species should be fierce and result in exclusion at broad spatial scales (Bull, 1991; Godsoe, Franklin, et al., 2017). Indeed, these species rarely co-occurred during our study, whereas coyotes and fishers overlapped considerably with lynx. Because snowpack is expected to decline in the northeastern U.S. (Ning & Bradley, 2015) and elsewhere along the southern limit of lynx range (Mote, Hamlet, Clark, & Lettenmaier, 2005), the concern is that bobcat will outcompete lynx and contribute to ongoing range contraction along its lower limit (Koen, Bowman, Lalor, et al., 2014; Peers et al., 2013). Our study provides convincing evidence for this possibility and suggests that natural resource managers will need to consider innovative solutions to alleviate these biotic constraints or accept the change in distributions.

Because biotic interactions are important along lower limits, climate envelope models might provide inaccurate predictions, especially given that novel conditions are expected from climate change that may dramatically alter community dynamics. Provided that climate mediates competition between highly similar species (e.g., lynx and bobcat), climate envelope model might capture relative changes in carnivore distributions. However, suitable habitat conditions, that provide prey for carnivores, will likely change at a slower rate than climate (Wang, He, Thompson, Fraser, & Dijak, 2016) and potentially allow for population persistence in climate change refugia (Morelli et al., 2016). This asynchronous dynamic may be especially important for species such as martens that require a combination of abiotic and biotic factors to fulfill life-history requirements and are considered threatened by climate and land-use change (Carroll, 2007). We advocate using iRLT to disentangle these factors. Once direct and indirect effects are known, it can be used as a heuristic tool for understanding which management and conservation actions can be used to conserve threatened species and control those expected to win out.

Table 2.1 Description of predictor and response variables used in occupancy and structural equation model (SEM) analyses, including the category, variable name, variable type (ρ= detection probability; ψ = occupancy; SEM = structural equation model), data source and description, and hypothesized effect of each variable.

Category	**Variable Name**	**Analysis**	**Source**	**Description**	**Hypothesis**
Abiotic factors	Snow depth, Maximum snow depth, Snow duration	SEM	SNODAS; Barrett (2003)	SNODAS produces daily predictions of snow depth (cm) at the 1 km resolution across the conterminous USA and southern CA. We calculated average depth, average maximum depth, and average snow duration during the study (2014-2019).	Snowpack mediates competition between populations along upper and lower range limits.
Biotic factor	Biomass	SEM	McGarigal et al. (2017)	Predictions of above ground live biomass (metric tons/ha) at 30 m resolution in the northeastern USA. Biomass ranged from 0 (no forest) to 185 (mature forest) metric tons/ha. http://jamba.provost.ads.umass.edu/web/lcc/dsl/technical/DSL_documentation_disturbance_succession.pdf	Forest biomass (proxy for age) provides habitat for prey and predators, imparting bottom-up effects.
Observation covariates	Year	ρ, ψ	Data from this study	Year of survey (2014, 2015, 2016, 2017, 2018, 2019)	Detection and occupancy probability would vary by year due to several unmodeled factors.
	Week^2	ρ	Data from this study	Survey week of each year from 15 October - 16 May (30 weeks)	Detection varies linearly or curvilinearly over time.
	Site biomass	ρ	McGarigal et al. (2017)	Predictions of above ground live biomass (metric tons/ha) at 30 m resolution in the northeastern USA at the camera sites. http://jamba.provost.ads.umass.edu/web/lcc/dsl/technical/DSL_documentation_disturbance_succession.pdf	Site-level forest biomass (forest age in proximity of camera) influences detection of species.
	Time since camera check	ρ	Data from this study	Number of weeks since a camera was checked.	Detection would be higher closer to the time a camera was checked due to use of lures.
	Temperature	ρ	PRISM (Daly et al. 2008)	We used PRISM temperature data (4 km resolution) to calculate temperature (°C) at each camera site during each week.	Temperature would affect activity of animals and performance of cameras.
	Snow depth	ρ	SNODAS; (Barrett 2003)	SNODAS produces daily predictions of snow depth (cm) at the 1 km resolution across the conterminous USA and southern CA. We calculated average depth at each week and site during the study (2014-2019).	Snow depth would influence the activity and mobility of survey species.

Table 2.2 Range limit position (Lower, Upper) and predicted effect of abiotic and biotic covariates on each species included in SEMs. Detection/Non-detection data of carnivore and prey species from camera surveys conducted between 15 October–16 May from 2014–2019.

Species	**Limit**[a]	**Predictions**
Canada lynx (*Lynx canadensis*)	Lower L/A	+ Snowpack, Biomass, -bobcat, -coyote
American marten (*Martes americana*)	Lower L/A	+ Snowpack, +Biomass, -fisher, -red fox
red fox (*Vulpes vulpes*)	Cos	+ Snowpack, Biomass, -coyote
bobcat (*Lynx rufus*)	Upper L/A	- Snowpack, Biomass
coyote (*Canis latrans*)	Upper A	- Snowpack, Biomass
fisher (*Pekania pennanti*)	Upper A	- Snowpack, +Biomass
snowshoe hare (*Lepus americanus*)	Lower L	+ Snowpack, -Biomass
red squirrel (*Tamiasciurus hudsonicus*)	Lower L	+ Snowpack, +/-Biomass
ruffed grouse (*Bonasa umbellus*)	Lower L	+ Snowpack, -Biomass
moose (*Alces alces*)*	Lower L	+ Snowpack, -Biomass
Prey availability (Lower)**	Lower L	+ Snowpack, -Biomass
white-tailed deer (*Odocoileus virginianus*)	Upper A	- Snowpack, -Biomass
wild turkey (*Meleagris gallopavo*)	Upper A	- Snowpack, +/-Biomass
gray squirrel (*Sciurus carolinensis*)	Upper L/A	- Snowpack, +/-Biomass
porcupine (*Erithizon dorsatum*)	Upper A	- Snowpack, +/-Biomass
Prey availability (Upper)**	Upper	- Snowpack, -Biomass

[a] Upper or Lower latitudinal (L)/altitudinal (A) limit of a species range within our study area. Red fox were found throughout the region and considered cosmopolitan (Cos).

*Moose were considered a prey item for our study because of high mortality from winter ticks (*Dermacentor albipictus*) that occurred during our study (Jones et al., 2019), resulting in scavenging opportunities for carnivores.

**Prey availability is prey species richness (sum of posterior ψ for all prey species within respective groups).

Table 2.3 Direct and indirect effects (path coefficients) of snow depth on focal species (Canada lynx, *Lynx canadensis*; American marten, *Martes americana*) and competitors (bobcat, *Lynx rufus*; coyote, *Canis latrans*; fisher, *Pekania pennanti*).

Focal species (competitor)	Direct effect of snow depth on focal species	Direct effect of snow depth on competitor	Direct effect of competitor on focal species	Indirect effect of snow depth on focal species via competitor
Lynx (bobcat)	0.561	-0.992	-0.760	0.754
Lynx (coyote)	0.561	-0.262	-0.978	0.256
Lynx (fisher)	0.561	-0.273	-0.563	0.154
Marten (coyote)	1.629	-0.262	-0.574	0.150

Figure 2.1 The *a priori* directed acyclic graph of Interactive Range-Limit Theory (iRLT), illustrating the influence of snowpack (abiotic), unlinked biotic factors (prey and habitat availability), and biotic interactions (competition) on carnivores along upper and lower range limits. Black arrows represent predicted direct effects and consecutive arrows pointed in the same direction represent indirect effects. Indirect effects are calculated by taking the product of consecutive patch coefficients. For example, the product of the 2 negative path coefficients between "Snowpack", "Carnivores along upper limits", and "Carnivores along lower limits" equals a positive indirect effect. Dashed lines with double-sided arrows represent free covariances (ε1,2,3).

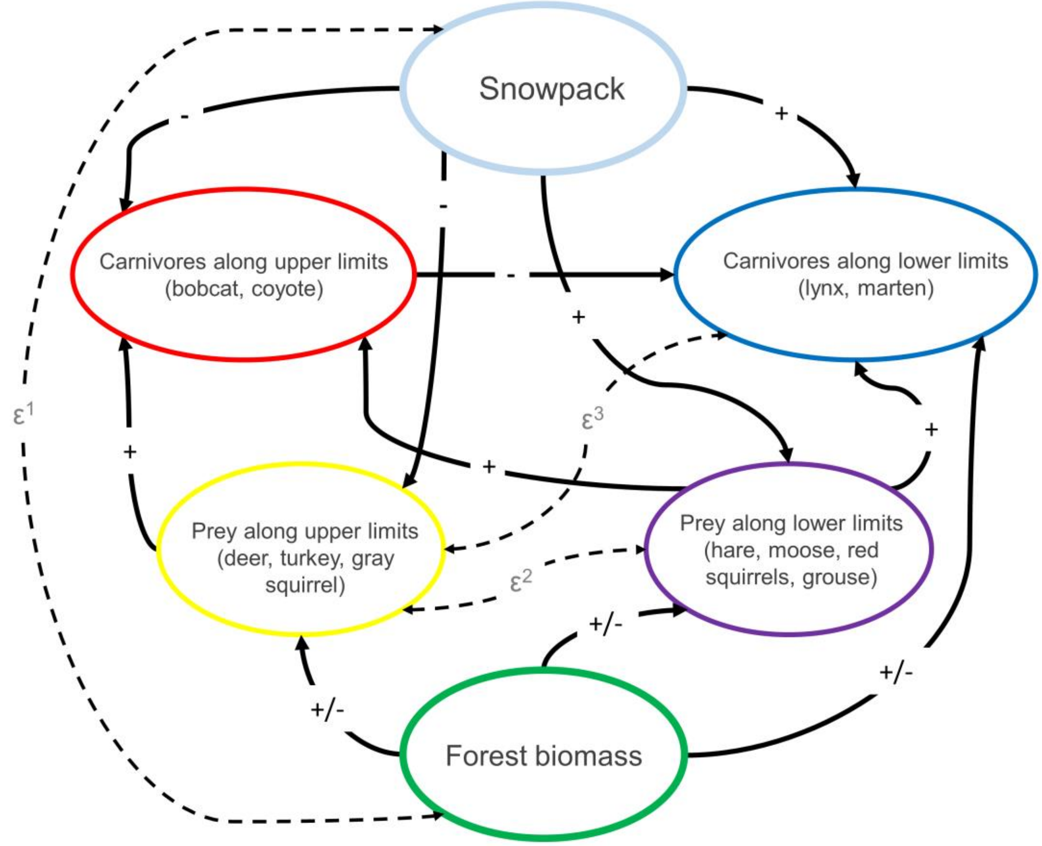


Figure 2.2 Location of 257 remote camera sites in New Hampshire and Vermont for studying mesocarnivore distribution dynamics. The camera trap method (upper left inset) includes a snow stake, feather, and remote camera placed 3–5 m away and pointed towards the snow stake.

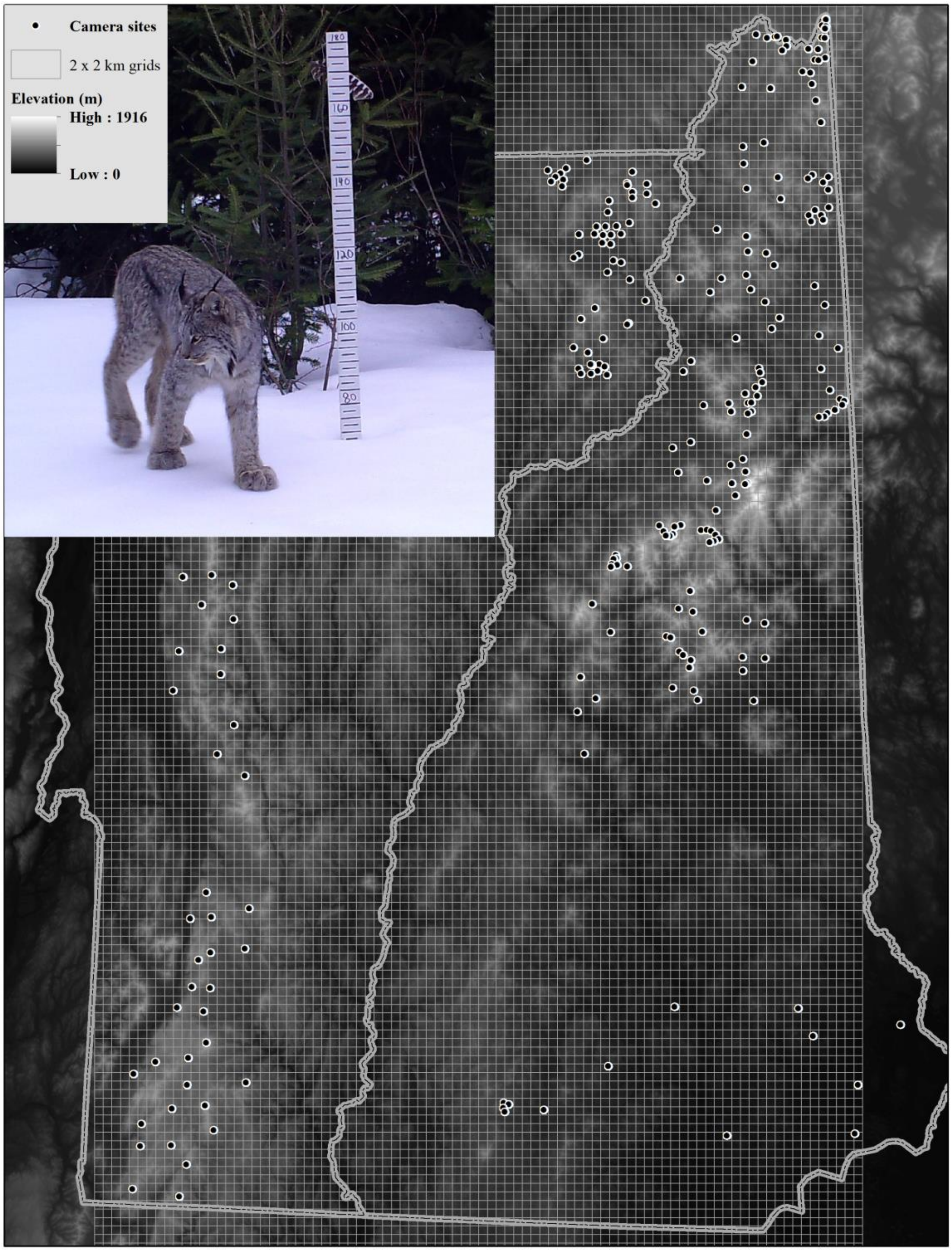


Figure 2.3 SEM for Canada lynx (*Lynx canadensis*) and bobcat (*Lynx rufus*) relative to direct and indirect effects of snow depth, prey availability, and forest biomass (metric tons/ha). Solid and unidirectional arrows represent direct effects and dashed bidirectional arrows signify correlated errors among variables. Thick lines indicate significant path coefficients, superscript symbols indicate significance level ($^{m}P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$), and conditional R^2 values (% of variation explained by the fixed and random effects) are listed within respective nodes. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols).

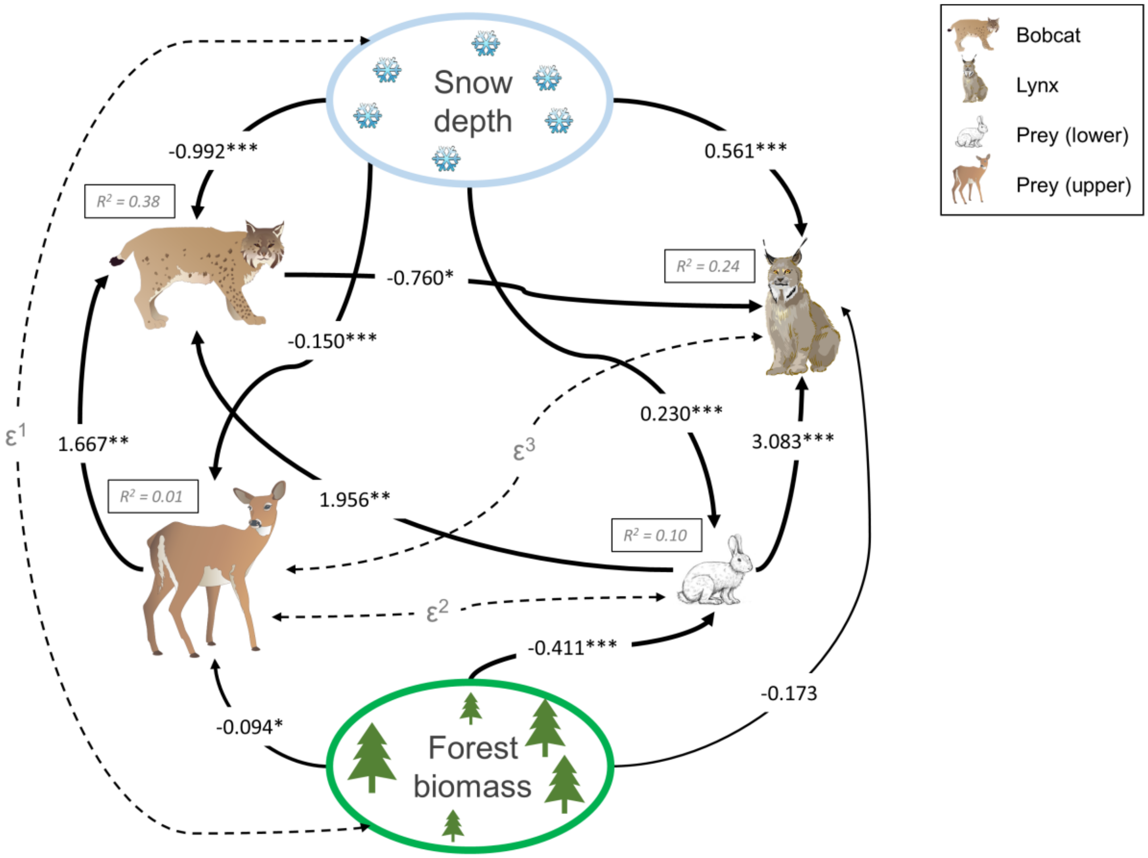
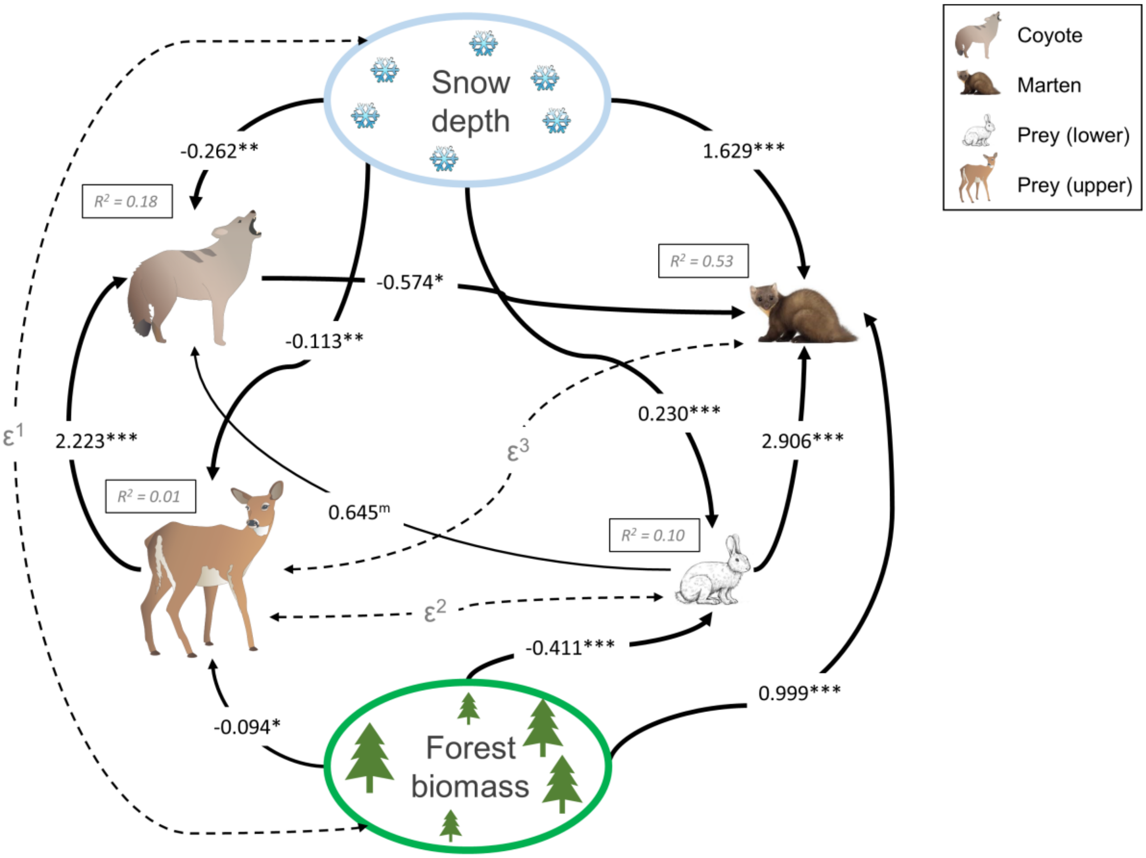


Figure 2.4 SEM for American marten (*Martes americana*) and coyote (*Canis latrans*) relative to direct and indirect effects of snow depth, prey availability, and forest biomass (metric tons/ha). Solid and unidirectional arrows represent direct effects and dashed bidirectional arrows signify correlated errors among variables. Thick lines indicate significant path coefficients, superscript symbols indicate significance level (${}^{m}P < 0.1$, $*P < 0.05$, $** P < 0.01$, $*** P < 0.001$), and conditional R^2 values (% of variation explained by the fixed and random effects) are listed within respective nodes. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols).



CHAPTER 3

A GREAT ESCAPE: THE ROLE OF CLIMATE, RESOURCE AVAILABILITY, AND DENSITY-DEPENDENT DYNAMICS ON AN ICONIC HERBIVORE ALONG ITS TRAILING EDGE

3.1 Introduction

Understanding the causes of range limits is a fundamental theme in ecology and evolution. Although climate is often considered an ultimate determinant of range limits, the role of biotic interactions can be equally important and is often a direct limiting factor, especially for populations along trailing edges (Louthan et al., 2015; Sirén & Morelli, 2019; Wisz et al., 2013). Previous studies have focused more on the role of competition whereas less attention has been given to predation, parasitism and resource-mediated density dependence (Holt & Barfield, 2009). Further, abiotic stress and resource availability can mediate biotic interactions and affect trophic levels differently, resulting in divergent population dynamics along distributional edges (Sirén *et al.* In Review; Sirén & Morelli 2019). These trophic differences are important to consider given that current and projected changes in climate and habitat will likely have profound effects on trailing edge populations (Hampe & Petit, 2005).

For mammalian herbivores that are more limited by predation or parasitism along trailing edges (see review in Sirén & Morelli 2019), variability in climate and resource availability can influence population dynamics and thus vulnerability to predation and parasitism (i.e., density-dependent predation). For example, some trailing edge populations of moose (*Alces alces*) are negatively affected by a warming climate through parasitism or disease (Jones et al., 2019; Murray et al., 2006; Uprecht, Koons, Hersey, Hobbs, & Macnulty, 2020). However, variations in resource availability can influence host density and infestations (Samuel, 2007) that potentially explains why some low-density moose populations persist at range edges (Samuel, 2007; Wattles & DeStefano, 2011; Wattles, Zeller, & DeStefano, 2018). Despite examples of this dynamic occurring in other systems at local scales (Reznick, Bryant, Roff, Ghalambor, & Ghalambor, 2004), the influence of climate and resource availability on density-dependent dynamics is rarely examined at the macroecological scale.

A new theoretical framework (Interactive Range-Limit Theory; iRLT) hypothesizes that abiotic stress mediates negative biotic interactions (e.g., competition, predation) for populations along lower range limits, yet the type of biotic interaction differs between carnivores and herbivores, resulting in unique processes and range-limit patterns for each trophic level (Sirén & Morelli, 2019). Existence at low-density provides herbivores a refuge from predation and parasitism, allowing them an escape from specialist predators along their lower limits. This idea, hereafter referred to as the Great Escape Hypothesis (GEH), is similar to Janzen-Connell effects (see review in Comita et al., 2014) but applied to primary consumers at the geographic scale. Briefly, Janzen-Connell effects are density- or distance-dependent processes that explain predation of seeds/seedlings of plants by specialist predators at local scales; seeds/seedlings in areas of low seed density or further away from a parent plant have higher survival (Comita et al., 2014). The density-dependent hypothesis of Janzen-Connell effects (i.e., the Escape Hypothesis: Howe & Smallwood, 1982) is akin to a Type III functional response associated with generalist predators (Holling, 1959; Murdoch, 1969; Oaten & Murdoch, 1975); specialist predators are able to hunt their prey to very low numbers but at the detriment of their own survival (Type II functional response), but generalist predators prey-switch when densities of a particular prey become too low (Type III functional response), allowing low-density prey to escape predation.

There are several assumptions and conditions that underpin GEH. First, GEH assumes that populations living in resource-poor environments will exist at lower densities but have higher survival due to Type III density-dependent predation (Reznick et al., 2004), yet the latter is contingent on the quality of matrix habitat. Consequently, populations will not vary as much as those living in resource-rich environments that attract predators (Hendry, 2017). Second, trailing edge populations will typically occupy habitats that are more fragmented than those in the core of their range (Pironon et al., 2017). Finally, density-dependent processes, that are commonly evaluated by community ecologists at local scales, are consistent across several spatial scales (i.e., local, landscape, and geographical). In summation, the combination of resource availability and density-dependent dynamics will allow prey species to escape predation and extend ranges farther towards the equator than their specialist counterparts. Although there is support in the literature for GEH, especially within aquatic ecosystems (Griffen & Williamson, 2008; Seitz et al., 2001), its predictions have yet to be explicitly tested using empirical data.

We investigate the generality of Janzen-Connell effects by extending the idea to multiple trophic levels, with a specific focus on snowshoe hares (*Lepus americanus*), using field data collected during a 6-year period (2014–2019) in the northeastern U.S. Snowshoe hares are a primary prey species for many carnivores in North America and have been the focus of intensive ecological study over the past century (e.g., Krebs et al., 2001). They are a model organism for understanding population dynamics and how snow-adapted species might respond to climate change (e.g., Griffin & Mills, 2009; Mills et al., 2018, 2013; Zimova et al., 2018). Identifying mechanisms influencing demography of peripheral populations of hares may provide information for how other prey species respond to climate and land-use change. This may be especially important in the northeastern U.S. where montane forests (Sprugel & Bormann, 1980; Sprugel, 1976) provide optimal climate and habitat refugia for hares and the carnivores dependent on them (Carroll, 2007; Hoving et al., 2005); yet, population dynamics of hares in this region are largely unknown.

We asked two questions: 1) What factors determine the southern range limit of snowshoe hares? and 2) What factors influence demography and life history of southern populations and thereby mediate the trailing edge? In accordance with iRLT, we hypothesized that snow would mediate distribution dynamics of snowshoe hares because it would affect survival and therefore abundance (Table 3.1). Accordingly, we predicted that snow duration would have a positive effect on hare distribution, similar to other studies (Burt et al., 2017; Sultaire, Pauli, Martin, Meyer, Notaro, et al., 2016), because of the increased survival advantage afforded via coat color camouflage (Wilson et al., 2018; Zimova et al., 2016) and associated ability to escape predators (Bowler, Krebs, O’Donoghue, & Hone, 2014). Second, we hypothesized that the availability of optimal habitat (regenerating forest) would exert a strong bottom-up effect on the distribution and abundance of hares (Holbrook, Squires, Olson, Lawrence, & Savage, 2017; Litvaitis, Sherburne, & Bissonette, 1985; Sultaire, Pauli, Martin, Meyer, & Zuckerberg, 2016), yet this would elicit density-dependent predation. Following this logic, we predicted that hares would have higher survival in low-resource environments (i.e., low-resources = low density hares) due to a Type III functional response (density-dependent predation) by generalist carnivores such as coyotes (*Canis latrans*) that are common along the southern edge of the range of snowshoe hares (Chan et al., 2017). Accordingly, we predicted that hare populations would not fluctuate in these environments due to a low-density refuge from predators. We further evaluated GEH by comparing parasite loads (namely rabbit ticks, *Haemaphysalis leporispalustris*) between populations living in high- and low-resource environments. Ultimately, we hypothesized that a combination of climate and resource conditions allow hares to persist along the trailing edge of their range in the northeastern U.S.

3.2 Materials and Methods

3.2.1 Study area

Our study area was located in the northeastern U.S. within the states of New Hampshire and Vermont (Fig. 3.1). This area is part of the northern hardwood and boreal forest transition zone (Goldblum & Rigg, 2010) and includes the highest peaks of the northeastern U.S. Boreal forest was generally found at higher elevations and at lower elevations in the north. The climate of the region is maritime with mild and rainy summers and cold winters with variable snowpack (Davis et al., 2013). Annual precipitation varies from 101–160 cm and snowfall ranges from 244–406 cm, with deeper snow at high elevation and northern regions (Davis et al., 2013; USDA, 2007). July is the warmest month averaging 18°C (11°C to 27°C) and January the coldest month averaging -11°C (-15°C to -2°C; USDA 2007).

Primary predators of hares in the study area included Canada lynx (*Lynx canadensis*), American marten (*Martes americana*), bobcats (*Lynx rufus*), red fox (*Vulpes vulpes*), coyotes (*Canis latrans*), fisher (*Pekania pennanti*), weasels (*Mustela spp.*), northern goshawks (*Accipiter gentilis*), and great-horned owls (*Bubo virginianus*). Lynx and marten were primarily located in the north, especially at higher elevations, whereas other predators were more widespread, except for bobcats that were typically found at lower elevations and farther south (Sirén *et al.* In Review).

3.2.2 Approach

To study factors influencing hare distribution, we used remote cameras that spanned a broad elevational (3–1,487 m) and latitudinal (42.8–45.3°N) gradient that was representative of the climate and dominant forest cover types and management regimes of the northeastern U.S. (Table 3.1, Fig. 3.1). For our demographic study, we sampled a variety of conditions that snowshoe hares experience, choosing 3 different regions (White Mountain National Forest [WMNF], Nulhegan Basin [NB], Connecticut Lakes Region [CL]) that varied in snowpack and resource (habitat) availability (Table 3.2, Fig. 3.1). The WMNF was the southernmost and highest elevation region (Table 3.2, Fig. 3.1), containing some of the oldest forests and deepest snowpack in the northeastern U.S. (Foster & D'Amato, 2015; Seidel et al., 2009). Consequently, we considered the WMNF to be the low-resource region, as older forest is not considered prime habitat for hares in eastern North America (Hodson, Fortin, & Belanger, 2011; Homyack, Harrison, & Krohn, 2007). NB was the mid-latitude and lowest elevation region (Table 3.2). It was dominated by spruce (*Picea spp.*)-balsam fir (*Abies balsamea*) forest that had been extensively harvested following the spruce-budworm (*Choristoneura fumiferana*) epidemic in the 1970s and 1980s (Chen, Weiskittel, Bataineh, & MacLean, 2017). It had the shortest snow duration and shallowest depths compared to the WMNF and CL (Table 3.2). The CL was the northernmost and mid-elevation study region. It was similar to the NB in forest composition and age yet had deep snow and long winters like the WMNF region (Table 3.2). We considered the CL and NB regions to be resource-rich regions because hares typically have higher abundance in regenerating spruce-fir forests (Litvaitis et al., 1985).

We monitored populations in all 3 regions using pellet surveys to index relative density (Hodges & Mills, 2008; Litvaitis, Sherburne, & Bissonette, 1985), sampling 60 stands that were representative of each region and the entire study area (Tables 3.1–3.2, Fig. 3.1). We chose 2 of these regions (WMNF, NB) to live-trap hares to estimate density, space use, survival, and collect reproductive and morphometric data (Tables 3.1–3.2, Fig. 3.1).

3.2.3 Hare distribution

We used data from 257 camera-trap sites operating from 9 January 2014–12 July 2019 to evaluate factors influencing hare distribution (Fig. 3.1). Cameras were spaced 2.90 ± 0.15 (SE) km apart and set to take 1–3 consecutive pictures every 1–10 sec when triggered, depending on the brand and model. The spacing distance of cameras greatly exceeds average space use and dispersal distances of hares (Homyack, Harrison, Litvaitis, & Krohn, 2006; Mills et al., 2005). Each site included a remote camera positioned facing north on a tree, 1–2 m above the snow surface, and pointed at a slight downward angle towards a stake positioned 3–5 m from the camera. A global positioning system (GPS) (Garmin GPS 62/64s, Garmin International, Olathe, KS, USA) was used to mark the location of each site when the position error of the GPS was <10 m. Commercial skunk (*Mephitis mephitis*) lure and wild turkey (*Meleagris gallopavo*) feathers were used as attractants and placed directly on the stakes. Cameras were checked on average 3 (range = 1–9) times each year to download data, refresh attractants, and to ensure cameras were working properly. For more information on the camera method see Sirén et al. (2018).

We modeled snowshoe hare distribution using single-season occupancy models (MacKenzie et al., 2017). To be consistent with snowshoe hare relative density surveys (see "Population surveys" subsection below), we used camera data from the leaf-off period (16 October–15 May). Camera data were organized into weekly occasions and for each occasion we recorded detection-nondetection of hares. We included these data in a single-species occupancy modeling framework (MacKenzie et al., 2017) to estimate weekly detection probability (ρ) and site occupancy (ψ) using the unmarked package (Fiske & Chandler, 2011) in R (R Core Team, 2019). Because we used data from multiple years (2014–2019), we used a stacked design that included the year of sampling as a fixed effect for detection and occupancy.

We used a suite of abiotic and biotic variables to evaluate detection and occupancy probability (Table A1 in Appendix C). Specifically, detection probability was modeled as a function of temperature, snow depth, site-level biomass (metric tons/ha), number of weeks since a camera was checked, and the Julian week of the year. For occupancy, we evaluated mean and maximum snow depth (cm) and the duration of snow cover (days) as abiotic covariates, and above ground live biomass (metric tons/ha) of the 3 major forest cover types of the region (boreal forest, mixedwood forest, hardwood forest) as biotic covariates. We used PRISM data for temperature (Daly et al., 2008) and

SNODAS data for snow depth (Barrett, 2003); both products provide daily predictions at the 4 km (PRISM) and 1 km (SNODAS) spatial resolution. Habitat covariates were created using 30 m resolution, regional land cover and forest biomass datasets (McGarigal, Compton, Plunkett, DeLuca, & Grand, 2017a; McGarigal et al., 2017b). The forest biomass dataset, used for modeling detection and occupancy probability, uses forest inventory analysis data and remotely sensed data of forest disturbance and succession to predict above ground live biomass for the northeastern U.S. for the year 2012 and is considered a reliable proxy of age for most forest cover types at the 30 m resolution (McGarigal et al., 2017b). Because snowshoe hares are influenced by forest age at a variety of scales (Hodson et al., 2011; Thornton, Wirsing, Roth, & Murray, 2013), we considered forest biomass as a candidate covariate for evaluating detection and occupancy probability. We used the ‘overlay’ function in the raster package (Hijmans et al., 2015) to create biomass layers for each cover type (boreal forest, mixed-deciduous, deciduous). We smoothed the snowpack and habitat occupancy layers using a Gaussian kernel function with a bandwidth that was relevant to the scale of our occupancy sampling (4 km^2 grids); site-level biomass was smoothed to a scale that we assumed influenced detection probability (90 m). Finally, we used the ‘extract’ function in the raster package to extract these values from the camera site locations to use as predictors for modeling detection and occupancy probability.

Prior to modeling we screened all detection and occupancy covariates for multicollinearity using Pearson’s correlation (r) and variance inflation factors (VIF), removing covariates from the same model if $r > 0.5$ or VIF >2 (Zuur, Ieno, & Elphick, 2010). Detection covariates were all weakly correlated ($r < 0.5$) and had low VIF scores

(VIF <2) so we allowed all combinations in models. Abiotic covariates used for modeling occupancy, on the other hand, were all highly correlated (*r* = 0.71, 0.88, 0.92) and had high VIF scores (VIF >2) so we evaluated each separately. Biotic covariates used for occupancy modeling were weakly to strongly correlated (*r* = -0.72, -0.39, -0.15, -0.11, 0.20, 0.48); we took steps to ensure that none of the correlated predictors were included in the same models. Finally, none of the abiotic and biotic covariates were highly correlated so we evaluated all possible combinations, using the sets of abiotic and biotic variables that had low VIF scores.

To determine the best performing detection and occupancy models, we employed a 2-stage approach. First, we evaluated factors that influenced detection by fitting a global occupancy model which we held constant. We fitted 'Week' as a second-order polynomial as we expected a non-linear relationship between detection and time for hares. After determining the best fitting detection model, we held it constant to evaluate factors that influenced occupancy. We evaluated all possible combinations of covariates given constraints from multicollinearity, resulting in a total of 40 models. Detection and occupancy models were evaluated using Akaike Information Criterion (AIC) scores. We chose the most parsimonious abiotic-biotic model within 2 AIC units. We considered a beta coefficient to have a significant effect if its 95% confidence intervals did not overlap zero. Finally, to determine how well the models fit the data, we conducted goodness-of-fit tests using the 'parboot' function in the unmarked package, running 500 bootstrapped iterations of the top detection model. We considered the top model to fit the data if the summed square of residuals (SSE) of the top model were within the distribution of the bootstrapped SSE (Kéry & Royle, 2015).

3.2.4 Population surveys

To evaluate density and population fluctuations, we established snowshoe hare fecal pellet plots within forested stands in the WMNF, NB, and CL regions (Fig. 3.1). We initially selected stand types based on purported high density of hares (spruce-balsam fir flats, spruce-fir uplands, krummholz, montane balsam fir, and montane spruce-fir) and those common in the region (northern-hardwood spruce-fir, and northern hardwood forest) using a forest classification system for the region (Sperduto & Nichols, 2012). We established 2-11 (mean = 5.5 ± 0.8) replicates of each stand type for a total of 60 stands overall. Forest stand types were delineated from GIS vector databases collected and maintained by state, federal, and private landowners, and cross-referenced with the National Land Cover dataset (Homer et al., 2015) when the accuracy of the cover type was uncertain. We attempted to maintain similar site conditions between stands (slope, aspect, soil type) but this was difficult due to the sampling requirements (≥45 plots/stand; Hodges & Mills 2008) and highly variable mountainous terrain in the WMNF. We also attempted to select stands that were of similar age classes as hare density is influenced by a broad spectrum of age classes (Hodson et al., 2011; Sullivan, Sullivan, Lindgren, & Ransome, 2012); the range of age for stands was 25–60 yrs in NB and CL, and 89–295 yrs in WMNF.

We used ArcMap 10.3 (ESRI, Redlands, California, USA) to establish stand boundaries and the Fishnet tool in ArcMap to establish plot locations within stands. Stands were either 18 ha (540 m x 340 m) or 20 ha (590 m x 340 m), including a 70-m buffer to reduce edge effects (Newbury & Simon, 2005), and spaced >500 m apart to meet assumptions of independence (Fig. A1 in Appendix C), as the average diameter of snowshoe hare home ranges or mean dispersal distances are less than this threshold throughout its range (Feierabend & Kielland, 2014; Homyack et al., 2006; Mills et al., 2005). Each stand contained 5 parallel transects with 9–10 plots all spaced 50 m apart, resulting in 45–50 plots/stand (Fig. A1 in Appendix C). Our classification scheme of stand types and seral classes resulted in 17 early successional stands in the NB (2 early regenerating hardwood, 3 early regenerating mixedwood, and 12 lowland spruce-fir), 11 early successional spruce-fir stands in the CL, and 32 mature stands in the WMNF (15 high elevation spruce-fir, 7 mixedwood, 6 lowland spruce-fir, and 4 hardwood). Although sample size was low for regenerating hardwood stands, the variance was very low for pellet densities in this forest type regardless of the age class we sampled.

Pellet plots were counted and cleared biannually at established stands to index leaf-off (16 October–15 May) density. We also conducted pellet surveys during the leaf-on season (16 May–15 October) to be consistent with other studies in the region that counted pellets biannually to account for potential decomposition (Homyack et al., 2006). However, we only used pellet plot data from the leaf-off period because it is more correlated with density of adults that survived the previous winter (Homyack et al., 2006). Sampling began at the WMNF in the fall of 2014, the spring of 2015 for the NB, and in the fall of 2017 for the CL region. Plots were established using GPS maps that contained stand and plot numbers. Technicians travelled to each GPS plot location and drove a 0.5–1 m wooden stake in the ground when the GPS position error was <10 m. Pellets were then counted and cleared within a 56-cm radius (Hodges & Mills, 2008; Murray, Roth, Ellsworth, Wirsing, & Steury, 2002) of each stake using a wooden dowel as a guide. Pellets that were either decomposing or had moss were not counted and every other pellet located on the 56 cm boundary was tallied. Although counts on uncleared plots are a reliable index of relative hare density (Hodges & Mills, 2008; Holbrook et al., 2017; Lewis, Hodges, Koehler, & Mills, 2011), we do not report on pellet data that was collected when stands and plots were first established for each region. After the spring 2017 field season, we stopped counting pellets in 11 stands in the WMNF and 3 stands in the NB that consistently had very low to zero pellet counts. This strategy has been employed elsewhere to increase sample size in productive stands (Mills et al., 2005) and allowed us to establish the CL region.

During spring and fall surveys from 2015–2019, we counted and cleared 839 pellet plots in 17 stands in the NB (3 mixedwood, 6 spruce-fir flats, 6 spruce-fir upland, and 2 hardwood stands), 1,535 plots in 32 stands in the WMNF (2 krummholz, 6 high elevation balsam fir, 6 high elevation spruce-fir, 8 mixedwood, 6 lowland spruce-fir, and 4 hardwood stands) and 495 plots in 11 stands in the CL region (11 spruce-fir stands; Table A2 in Appendix C). We used data from these surveys to evaluate the strength of the pellet-hare index (Text A1 in Appendix C) and to test hypotheses related to resource availability and population fluctuations.

3.2.5 Demographic data

We live-trapped and radio-collared hares to 1) collect morphometric and reproductive data, 2) evaluate the pellet-hare index, 3) estimate stand- and landscape-scale density, 4) obtain telemetry locations for evaluating space use, and 5) identify factors influencing survival (Table 3.1). Trapping followed leaf-off pellet count surveys and the effort occurred from 20 June–13 August 2016 and the following year from 6 June–28 July 2017. We placed live-traps (*n* = 25–50) at or within 5 m of pellet plots (Fig.

A2 in Appendix C), baited traps with alfalfa cubes and pellets and apple slices and used vanilla extract to lure animals inside the traps. Traps were set each day between 1600 h–2000 h and checked the following day between 0600 h–1000 h; we closed traps during the middle of the day to avoid bycatch. Upon capture, hares were sexed, ear-tagged, and radio-collared each with lightweight (26 g) VHF collars (ATS, Isanti, Minnesota, USA); only adults were processed (juveniles can be differentiated using hind foot measurements; Litvaitis, 1990). Morphological measurements and reproductive status were also recorded. Differences in body mass (g) were compared between adult males using one-way analysis of variance; females were excluded because pregnancy can confound estimates of body mass. Leveret (juvenile hares) captures were recorded but individuals were not identified. To compare reproductive output between regions, we considered the ratio of adult-females to leveret captures as an index of reproduction. We compared differences in the frequency of adult females and leveret captures between regions using a Fisher's-exact test of independence; alpha was set at 0.05 and the test was performed using the 'fisher.test' function in R (R Core Team, 2019). Finally, we recorded the presence of rabbit ticks (*Haemaphysalis leporispalustris*) by inspecting the ears of each captured individual (Keith & Cary, 1990). All activities associated with trapping, handling, and radio-collaring were done in accordance with an animal care and use protocol (University of Massachusetts, Amherst, IACUC Protocol # 2016-0024, Text A4 in Appendix C).

3.2.6 Space use

Space use is commonly used to evaluate the availability or quality of habitat resources (Andreassen, Hertzberg, & Ims, 1998) with larger or longer movements indicating lower resource availability (Ims, Rolstad, & Wegge, 1993; Sirén, Pekins, et al., 2016). To evaluate our prediction that low resource availability in the WMNF region would result in longer movements, we conducted telemetry monitoring on a weekly basis during the leaf-on season (16 May–15 October) of 2016. We obtained locations by triangulating hares, taking ≥3 bearings within 30 min; outermost bearing angles were 60°–145° and adjacent bearings were ≥30°. Occasionally, we obtained locations by homing and visual confirmation, or via biangulation; in the latter case, we only used bearings with angles that ranged from 60°–120°, ideally 90° apart. For visual locations, we used a GPS to estimate the bearing and distance we were from the animal. We used telemetry software (LOAS; Ecological Software Solutions, Hegymagas, Hungary) to estimate locations using a maximum likelihood method. We chose to increase the sample of radio-collared animals rather than the number of locations/animal to provide population-level inference of space use (Ivan, White, & Shenk, 2014). We provide the sample size, mean (± SE) number of locations, and mean maximum distance moved (MMDM) for the NB and WMNF; differences in means between regions were compared using a one-way analysis of variance.

3.2.7 Stand- and landscape-scale density

Because we found a moderately strong correlation between pellet and hare density (see Text A1 in Appendix C), indicating pellet surveys were a reliable index of density, we used pellet data to evaluate bottom-up factors influencing density. This approach allowed us to use data from 60 stands to evaluate stand types that were most productive for hares in the region. We modeled the pellet counts using a negative binomial generalized linear mixed models (GLMM) with a log link function in the glmmTMB package in R (Brooks et al., 2017; R Core Team, 2019). We chose this probability distribution because it is well-suited for count data that has a high number of zero counts and a high mean that does not equal the variance (O'Hara & Kotze, 2010). Further, prior evaluation of other probability distributions (e.g., Poisson, zero-inflated Poisson) using Akaike Information Criterion (AIC) indicated it performed considerably better (AIC of other distributions were >443.1 AIC units compared to the negative binomial model). For each model, we included the "stand" and "plot" as a nested random effect to incorporate for potential spatial correlation between stands and plots and included the "year" of sampling as a random effect to account for potential correlation among years. To account for differences in accumulation rates since the time plots were last sampled, we fit the log number of days ("day") as an offset variable. We modeled counts (adjusted for time) as a function of stand type and region (WMNF, CL, NB) to evaluate bottom-up factors influencing stand- and landscape-scale density; landscapes were defined as all the stands within a region (i.e., WMNF, NB, and CL). We made comparisons between stand- and landscape-levels using Tukey-adjusted tests with the "emmeans" package in R (Lenth, Singmann, Love, Buerkner, & Herve, 2019). Finally, we also evaluated spatial autocorrelation of model residuals (rSAC) using a Moran's-I test and evaluated significance at the 95% confidence level. Because we detected rSAC for stand and landscape models, we fit an exponential spatial covariate that incorporated the locations of each plot. We chose the exponential correlation structure because other terms failed to converge (e.g., Gaussian, Matern) and subsequent Moran's-I tests revealed that this covariate resolved issues of rSAC.

3.2.8 Population fluctuations

To evaluate annual population fluctuations for each region, we employed the same modeling approach used to evaluate bottom up factors on relative hare density (i.e., a negative binomial GLMM), except we switched “year” from a random to a fixed effect to evaluate differences in years. Further, because we also found evidence of rSAC for these models, we also included an exponential term to account for correlated errors. We had 4 years of data for the WMNF (2015–2018) and the NB (2016–2019) and 2 years for the CL region (2018–2019). Initial comparisons were made with the reference category, which was the first year of monitoring for each region, and then Tukey-adjusted tests were conducted using the “emmeans” package to evaluate differences among years.

3.2.9 Survival

To evaluate factors influencing survival, we captured hares within established stands in the CL (*n* = 6) and WMNF (*n* = 5) that spanned the density of hares, as measured using pellet surveys, for each region and radio-collared each with lightweight (26 g) VHF collars (ATS, Isanti, Minnesota, USA). These individuals were monitored weekly throughout the study to estimate seasonal and annual survival rates; when possible cause-specific mortality was assessed via necropsy (Boutin, Krebs, Sinclair, Anthony, & Smith, 1986; Ivan et al., 2014). Survival rates were compared between regions and sexes to determine which factors most influenced population dynamics. To determine cause of death for mortalities we followed a standard protocol (Text A2 in Appendix C).

We reported survival rates as the percentage of animals that were repeatedly tracked through each year of sampling (16 May 2016–15 May 2017; 16 May 2017–15 May 2018) and made comparisons between the NB and WMNF. We chose this annual calendar because it corresponded with the timing of our trapping efforts. We used Cox regression models with the R package 'survival' (R Core Team, 2019; Therneau & Lumley, 2017) to model weekly survival using the following covariates: region (WMNF, NB), and sex (M, F). We evaluated the significance of parameter estimates at the 95% confidence level. Further, we tested for violations of proportional hazards with a Chi-square test using the 'cox.zph' function in the survival package, where a $P < 0.05$ indicates a violation of proportionality and poor fit (Therneau & Lumley, 2017).

3.3 Results

3.3.1 Hare distribution

We detected hares 2,500 times at 169 of the 257 camera sites (naïve occupancy = 0.66) from 2014–2019. Overall, weekly detection probability was high ($\rho = 0.23$) and there were several factors that influenced detection probability (Fig. A2 in Appendix C). Site occupancy was also high ($\psi = 0.81$) and the top model included snow duration and forest biomass (Table A1 in Appendix C); hare occupancy was positively associated with snow duration and negatively associated with forest biomass (Table 3.3; Fig. 3.2). Additionally, there was variation in occupancy among years, with the lowest occupancy occurring during the winters of 2015–2016 and 2018–2019 compared to the reference category (2013–2014; Table 3.3, Fig. A3 in Appendix C). The summed square of residuals (SSE) of this model was within the distribution of the bootstrapped SSEs ($P = 0.08$), indicating it fit the data well (Fig. A4 in Appendix C).

3.3.2 Demographic data

We trapped a total of 5 stands in the NB during the summer of 2016 (Table A3 in Appendix C). We captured 38 adult hares (21 M; 17 F) 71 times (*n* = 33 recaptures) and recorded 41 leveret captures (Table 3.4). During the summer of 2017, we trapped 3 stands, including one that was trapped the previous summer (9SFF4, 9SFF6, 9SFU1). We captured 22 adult hares (12 M; 10 F) 54 times (*n* = 32 recaptures) and recorded 14 leverets (Table 3.4).

We trapped 7 stands in the WMNF (Table A3 in Appendix C) during the summer of 2016, capturing 14 adult hares (7 M; 7 F) 24 times (*n* = 10 recaptures) and recording 9 leveret captures (Table 3.4). During the summer of 2017, we trapped 2 stands from the previous summer (6HSF3, 6SFW1) and captured 6 adult hares (2 M; 4 F) 12 times (*n* = 6 recaptures); however, no leverets were captured during trapping efforts.

Overall, we detected demographic differences between regions during the 2 years of live-trapping and capture. Reproduction in the NB was significantly higher (*P* = 0.04) than the WMNF, indicating that adult females produced twice as many leverets in the NB (Table 3.4). We detected numerous ticks on each hare in the NB, but only counted one tick on one individual in the WMNF. Body mass of males was 5 g larger in the WMNF (1389 ± 48 SE g), but this difference was not significant (*P* = 0.96).

3.3.3 Space use

We radio-collared 30 hares in the NB and 12 in the WMNF during the leaf-on season of 2016 (16 May–15 October) to evaluate space use. We recorded 206 locations (6.9 ± 0.3 SE locations/hare) and 97 locations (8.1 ± 0.7 SE locations/hare) in the NB and

WMNF, respectively. Mean maximum distance moved (MMDM) was shorter on average in the NB (186 ± 31 m; $\beta = -83.65$, $t = -2.742$, $P = 0.007$) than the WMNF (269 ± 25 m).

3.3.4 Stand- and landscape-scale density

Relative hare density, as indexed using pellet data, was significantly higher in the early successional conifer-dominated stands of the NB and CL compared to most other stand types (Fig. 3.3), with most stands in the WMNF having low pellet and absolute density (Tables A2–A4 in Appendix C). Accordingly, landscape-scale density was significantly lower ($P < 0.05$) in the WMNF compared to the NB and CL for pellet density (Table A5 in Appendix C, Fig. 3.3, inset) or absolute density (WMNF vs. NB only; Table A7, Fig. A5 in Appendix C). However, although density was higher in the NB than the CL, these differences were not significant (Table A5 in Appendix C, Fig. 3.3, inset, Fig. 3.4).

3.3.5 Population fluctuations

We detected differences in population fluctuations between regions. Comparatively, density remained relatively stable in the WMNF with some differences between years (Table A6 in Appendix C, Fig. 3.4), yet density fluctuated greatly in the NB and CL (Table A6 in Appendix C, Fig. 3.4). Although differences were relatively small compared to NB and CL, density was significantly lower in the WMNF during 2017 compared to other years (Fig. 3.4). For the NB, density was lowest in 2016 and significantly higher in 2017 (Table A6 in Appendix C, Fig. 3.4). For the two years we monitored hares in the CL, density was significantly higher in 2018 than 2019 (Table A6 in Appendix C, Fig. 3.4).

3.3.6 Survival

We monitored a total of 66 adult hares from 21 June 2016–15 May 2018; of these only one was censored due to collar failure. The proportion of hares surviving the entire study was considerably lower for the NB (17%; 8 of 48 animals alive) than the WMNF (50%; 7 of 14 animals alive). Accordingly, weekly survival was significantly higher in the WMNF ($\beta = -1.004$, $z = -2.439$, $P = 0.0147$; Fig. 3.5) with 75% and 64% of hares surviving compared to 37% and 28% in the NB during 2016 and 2017, respectively. Sex was not an influential predictor of hare survival ($\beta = -0.058$, $z = -0.197$, $P = 0.843$). Tests for violations of proportionality indicated that models fit the data well for the region ($\chi^2 = 0.03$, $P = 0.86$) and sex ($\chi^2 = 0.005$, $P = 0.95$) models. Predation was the primary cause of mortality for both regions (62%; 29 of 47 mortalities; Table 3.5). Further, many of the mortalities that were categorized as unknown were likely due to predation. Most predation events were associated with terrestrial predators with few attributed to avian predation (Table 3.5). Finally, we identified the predator species on 6 occasions (2 coyotes, 2 fisher, 1 marten, and 1 bobcat) and the taxonomic family of the predator on a further 3 occasions (Table 3.5).

3.4 Discussion

Biotic interactions have long been considered a limiting factor for animal and plant populations along trailing edges (Darwin, 1859; Dobzhansky, 1950; MacArthur, 1984). We extended this theory and posited that abiotic stress can mediate biotic interactions, although the processes differ by trophic level (Sirén & Morelli, 2019). For herbivores, more limited by predation or parasitism (Hairston, Smith, & Slobodkin, 1960), density dependence has an integral role and can potentially counteract negative biotic interactions when population sizes are low (Seitz et al., 2001). We hypothesized that this dynamic extends to macroecological scales (i.e., the Great Escape Hypothesis; GEH) and explains why the trailing edges of some herbivore species extend beyond the range of their natural enemies (Sirén & Morelli, 2019). By integrating multiple data sources at different spatial scales collected during the same time frame, we show that density-dependent dynamics, mediated by climate and resource availability, have an important role for sustaining populations along trailing edges, supporting the GEH. We discuss our findings within the context of classical and emergent theories on range limits and population dynamics with implications for understanding how snowshoe hares and others might be affected by ongoing climate and habitat change.

According to iRLT, we hypothesized that abiotic factors, especially snow depth or duration, would influence the distribution of hares because of their unique adaptations to snow that aid in survival (camouflage and escape from predators; Bowler et al., 2014; Zimova et al., 2016). Our hypothesis was well supported; hare occupancy was positively associated with snow duration, corroborating past studies (Burt et al., 2017; Sultaire, Pauli, Martin, Meyer, Notaro, et al., 2016). Higher occupancy in regions with long and snowy winters was likely associated with higher survival rates from coat-color camouflage, which has been documented in other regions (Wilson et al., 2018; Zimova et al., 2016). Adding evidence to these findings, we documented significantly lower occupancy rates and the lowest density in the NB after the shortest snow winter of 2015–2016. However, abundance remained similar within the WMNF during the same time frame. Of note, occupancy was also low in 2019, which followed the most severe winter, yet this only appeared to have a negative influence on density in the northern CL region.

Indeed, severe winters can have a negative effect on hares due to decreased mobility (Kielland, Olson, & Euskirchen, 2010; Meslow & Keith, 1971), inaccessibility to browse (Keith et al., 1984; but see Kawaguchi & Desrochers, 2017), or reverse mismatch (i.e., hares are brown when snow is present; Zimova et al., 2019). All of these direct and indirect effects of snow on survival can translate into changes in occupancy and density of hares and suggest that an intermediate snowpack might be most optimal for hares (Kielland et al., 2010).

We also predicted that biotic factors, specifically forest biomass, would exert a strong bottom-up influence on the distribution and density of hares. Our results were well-supported; forests with low biomass (a proxy for early-regenerating forest) were positively associated with hare distribution. These findings are consistent with studies in the western U.S. that also identified habitat to have a strong bottom-up effect on hare distribution (Holbrook et al., 2017; Lewis et al., 2011; Sultaire, Pauli, Martin, Meyer, & Zuckerberg, 2016; Thornton et al., 2013). At a local scale, it was evident that regenerating boreal forest was driving snowshoe hare density. These findings are in agreement with previous work in eastern North America that indicate early-regenerating stands dominated by spruce-fir provide optimal hare habitat (food and cover) at the stand-scale, likely due to dense horizontal and vertical cover afforded by conifer saplings (Buehler & Keith, 1982; Homyack et al., 2007; Kawaguchi & Desrochers, 2018; Litvaitis et al., 1985). These forest structural attributes are found in a variety of seral stages, depending on region (Buehler & Keith, 1982; Laura C. Gigliotti, Jones, Lovallo, & Diefenbach, 2018; Griffin & Mills, 2009; Hodson, Fortin, & Bélanger, 2010) and influence larger scale patterns of occurrence and density (Holbrook et al., 2017; Lewis et al., 2011; Sultaire, Pauli, Martin, Meyer, & Zuckerberg, 2016; Thornton et al., 2013).

Interestingly, we found that forest biomass had a slightly stronger effect on hare occupancy than snow duration. Because there are relatively few studies that have evaluated the influence of abiotic and biotic factors on hare distribution, it is worth elaborating further. Our finding contrasts with hare studies in the midwestern and western U.S. (Holbrook et al., 2017; Sultaire, Pauli, Martin, Meyer, Notaro, et al., 2016), potentially due to differences in sampling or the predator community. Unlike Sultaire et al. (2016), we did not quite sample beyond the southern limit of snowshoe hares. Prior studies have advocated the importance of sampling beyond the range limit to identify threshold responses (Louthan et al., 2015; Sirén & Morelli, 2019). However, Sultaire et al. (2016) used a binary classification of habitat (forest, non-forest) which may have reduced their power to detect bottom-up effects. Our study shows a strong selection towards a specific age class, like previous studies across the geographic range of hares (Litvaitis et al. 1985, Griffin and Mills 2009, Ivan et al. 2014). It is not clear why our analysis differed from Holbrook et al. (2017). Perhaps snow is more important for hares in these landscapes because lynx, a specialist predator of hares, was prevalent throughout their region whereas it only existed in the far northern part of our study area. Regardless of these regional differences, our work indicates the importance of biotic resources along trailing range limits, which is consistent with theoretical expectations (Sirén & Morelli, 2019). However, as we discuss in the following paragraphs, resource-rich environments come with a cost.

Our hypothesis that populations living in low-resource environments would have lower densities that would provide them a refuge from predation (i.e., GEH) was well-supported. Hares were at lower density in the WMNF and moved longer distances, presumably because of the patchy distribution of resources within this region. Further, hare populations did not fluctuate appreciably in the WMNF, likely remaining at carrying capacity given the limited resources. Consequently, this combination of factors likely contributed to higher survival compared to hares living in the resource-rich NB region. Adding support to GEH, we only found a single rabbit tick on one hare in the WMNF, whereas ticks were prevalent and often abundant on all hares captured in the NB during the course of the study. An alternative explanation for the lower mortality rates and near absence of ticks in the WMNF, other than density-dependence, was that winters were colder and snowier in the higher elevation WMNF compared to the NB. However, past studies found high mortality and parasitism of hares even in regions with long winters and deep snow (Campbell, Ward, & Garvie, 1980; Dashiell Feierabend & Kielland, 2015; Griffin & Mills, 2009); all of these populations were living in resource-rich environments. Moreover, other areas in the WMNF region within the same elevation range as the NB had similar climate, yet populations remained low and stable during the study. Further, the resource-rich CL region had similar climate to the WMNF, yet population size varied considerably like the NB region. Collectively, these findings provide support that bottom-up effects elicit density-dependent dynamics.

The population-level differences we observed are strikingly similar to past work in other systems that indicates how resource availability evokes density-dependent predation and differential population dynamics (Reznick, Bryga, & Endler, 1990;

Reznick et al., 2004). We found significantly lower reproductive output in the resource-poor WMNF region that had higher survival. Further, these populations did not fluctuate appreciably during 4 years of monitoring. According to life-history theory, populations experiencing low predation pressure will often exhibit K-type traits such as lower reproductive output and stable population size (Hendry, 2017). Perhaps the best example of this comes from Trinidadian guppies; populations living in low-resource environments experienced less predation and had low reproductive rates (Reznick et al., 1990; Reznick et al., 2004). Another trait influenced by predation is body size (Lomolino, 2005; McNab, 2010); populations experiencing lower predation can live longer and maximize available resources and attain larger body size. We did not find statistically significant differences in body mass between populations; males were only 5 g larger in the WMNF than the NB. Variation in body size among populations can be attributed to resource availability (McNab, 2010) and previous work has suggested that the larger body mass of southern hares is attributed to milder winters and longer growing season (i.e., higher net primary productivity; Gigliotti et al. 2019). Nevertheless, hares from our study were similar in size to other southern populations (see studies in Gigliotti et al., 2019)g, yet those in the WMNF were living in low resource conditions. Because our study was not designed to evaluate this hypothesis, further study is warranted.

We propose an alternative explanation as to why hares do not cycle in the southern part of their range. Based on our data, we suggest that changes in life-history traits (i.e., adult survival, reproductive output), caused by differences in resource availability and density-dependent predation, prevent populations from cycling in those regions. While this hypothesis contrasts to the refugium model (Griffin & Mills, 2009;

Wolff, 1980), both explain dampened cycles, via different causal pathways. The differences in demography between our study and those in the western U.S. (Griffin & Mills, 2009; Wirsing, Steury, & Murray, 2002) might be attributed to the quality of matrix habitat. Boreal forest in the western U.S. is naturally fragmented and surrounded by open habitat (Griffin & Mills, 2009), whereas boreal forest in the northeastern U.S. is intermixed with temperate forest (Goldblum & Rigg, 2010) that is likely more suitable matrix habitat. As predicted by the GEH, these conditions may provide a low-density refuge from predators (Sirén & Morelli, 2019) and afford a unique survival advantage compared to hares living in harsh matrix habitats of the western U.S. Clearly, more study is warranted to understand these dynamics. Studying hares in a region with milder winters dominated by neutral matrix habitat could provide stronger inference.

Of note, the disturbance regime of the montane forests in the WMNF have a long return interval and early-regenerating stands are patchily distributed (Lorimer & White, 2003; Sprugel, 1976); both of these factors contribute to stable and low hare densities. In a broader sense, these forest conditions, common in the WMNF, are representative of the older-aged temperate-boreal forests of the northeastern U.S. and likely similar to Pre-Columbian forests (Litvaitis, 2003; Lorimer & White, 2003). Thus, it is conceivable that hares, and other early-successional species such as moose, have persisted in this region for centuries at low density with occasional population spikes from large scale disturbances (e.g., fire, insect outbreaks, hurricanes). A low-density refuge provided by these forests may explain why some early successional species like hares persist in regions with unsuitable climate (e.g., Pennsylvania; Gigliotti, Diefenbach, & Sheriff,

2017) or the recent southward expansion of moose that are freed from high parasite loads when densities are low (Samuel, 2007; Wattles & DeStefano, 2011).

Our findings suggest counterintuitive forest management strategies for conserving prey populations along trailing edges. First, maximizing optimal habitat for hares could create a negative feedback loop, especially if high density populations are exposed to climate conditions that are unsuitable (e.g., short winters; Mills et al., 2013). For example, intensive forest management (e.g., large clear cuts) to increase hare densities could inadvertently elicit density-dependent predation which would only intensify during short winters when hare camouflage is compromised (Zimova et al., 2016), unless there is sufficient structurally complex habitat (Wilson et al., 2018). Of note, hare populations in the northeastern U.S., compared to other regions, are most vulnerable to mismatch (Zimova et al., 2019), likely due to the trend of shorter winters (Contosta et al., 2019). Thus management actions will need to consider the vulnerability of hares by region. However, landscapes dominated by older-aged forests could result in low density populations that are susceptible to demographic stochasticity and low genetic diversity (Cheng, Hodges, Melo-Ferreira, Alves, & Mills, 2014). Thus, it will be prudent to find a balance that maximizes density yet does not elicit a density-dependence response from predators, i.e., keeping abundance high enough but not too high. This approach (although likely challenging), along with novel strategies (e.g., evolutionary rescue; Mills et al., 2018) will need to be considered to help hares adapt to a changing climate and to balance the needs of other species with different habitat requirements.

Our study has several limitations that are worth noting. First, despite sampling across a broad spatial gradient with numerous replicates for each stand type within each region, we relied on pellet survey data for indexing density and population fluctuations. This approach has drawbacks, especially for studies with low pellet counts that are not as predictive of absolute density (Mills et al., 2005); however, we used a pellet plot design (m^2 circular plots) that performs better at low densities (Murray et al., 2002). Ideally, future studies should estimate density using capture-recapture models either from live-trap or genetic data (Cheng, Hodges, Sollmann, & Mills, 2017; Mills et al., 2005). Next, our survival analysis had a relatively low sample size, especially for the WMNF ($n = 14$ hares). We attempted to mitigate errors that arise from this problem by only fitting simple univariate models, as done previously (Gigliotti & Diefenbach, 2018; Kumar, Sparks, & Mills, 2018). Also, our index of reproduction (adult females to leveret captures) is fraught with several problems, including heterogeneity in the timing of birth pulses between study areas and differences in detectability among sites. Given these shortcomings, we suggest future studies to 1) use methods that more accurately represent the states of interest (e.g., density and reproduction) and 2) obtain higher sample sizes to test predictions of GEH.

Table 3.1 Description of hypotheses, predictions, and data used to evaluate the influence of climate and resource availability on snowshoe hare (*Lepus americanus*) demography.

Demographic parameter	Hypotheses	Predictions	Data source
Distribution	Snow determines, in part, the distribution of hares as it mediates survival (coat-color camouflage, escape from predators).	Occupancy is positively associated with snow duration.	Detection/non-detection data (weekly) from 257 cameras collected from 2014–2019 throughout New Hampshire and Vermont. Data were used to determine factors influencing distribution using site occupancy models.
	Forest age determines resource availability (food, thermoregulation) and thus the distribution of hares.	Occupancy is positively associated with early-regenerating boreal forest.	
Density	Snow determines snowshoe hare density because it mediates survival (coat-color camouflage, escape from predators).	Density is positively associated with snow duration from the previous winter.	Pellet surveys and live-trap data collected from 2015–2019 in the CL, NB, and WMNF. Pellet data were used as an index of abundance and live-trap data were used to estimate density using spatial capture-recapture models.
	Forest age determines resource availability (food, thermoregulation) and thereby hare densities.	Density is positively associated with early regenerating boreal forest.	
Population fluctuations	The quality and amount of optimal habitat determines snowshoe hare population fluctuations due to density-dependent dynamics.	Populations fluctuate more in resource-rich environments (early-regenerating boreal forest).	Pellet survey data collected from 2015–2019 in the CL, NB, and WMNF. Leaf-off pellet counts were used as an index of abundance.
Survival	Snow impacts survival because hares are a snow-adapted species (camouflage, fleeing predators).	Hare survival is positively associated with snow duration.	Survival data collected from radio-collared snowshoe hares from 2016-2018 in the NB and WMNF. Known fates of hares were used to model survival.
	The quality and amount of habitat affects snowshoe hare survival due to density-dependent dynamics.	Hare survival is lower in resource-rich environments due to density-dependent dynamics.	
Space use	Space use reflects habitat quality and resource availability.	Movements would be longer in resource-poor environments.	Telemetry relocation and live-trap data collected from radio-collared hares during the summers of 2016-2017 in the NB and WMNF.
Parasitism	Parasitism is associated with resource availability and density-dependence.	Parasitism is lower in resource-poor environments due to density-dependent dynamics.	Presence of ticks on the ears of hares captured from live-trapping during the summers of 2016-2017 in the NB and WMNF.

Table 3.2 Summary of mean (SD) latitude, elevation, and climate (1980–2009) of the regions (WMNF, NB, CL) used for monitoring snowshoe hare demography from 2014–2019.

Region[a]	Latitude (DD°)	Elevation (m)	Temp (°C)[b]	Snow duration (days)[c]	SWE (cm)[d]	Population monitoring (Years)	Demographic study (Years)
WMNF	44.34 (0.05)	836.91 (273.35)	4.25 (10.59)	187 (70)	110 (32)	2014-2018	2016-2018
NB	44.84 (0.02)	422.75 (61.05)	4.44 (11.34)	148 (67)	52 (18)	2015-2019	2016-2018
CL	45.16 (0.04)	712.00 (125.02)	3.14 (11.35)	184 (65)	115 (24)	2018-2019	N

[a] Regions are abbreviated as follows: WMNF = White Mountain National Forest; NB = Nulhegan Basin; CL = Connecticut Lakes.

[b] Temperature data (average annual values within each region) were obtained from gridMET (Abatzoglou, 2013).

[c] Snow duration and snow water equivalent (SWE) data (average annual values within each region) were obtained from Livneh (Livneh et al., 2015).

Table 3.3 Parameter estimates (Est), standard errors (SE), and probability statistics (P) for top performing single-species occupancy (ψ) models of snowshoe hares using camera trap data collected from 9 January 2014–15 May 2019 in New Hampshire and Vermont, USA. Significant relationships are highlighted in bold.

Parameter (ψ)	Est	SE	z	P(>|z|)
(Intercept)	1.426	0.374	3.807	0.000
Year 2015	-0.108	0.562	-0.192	0.848
Year 2016	**-0.964**	**0.45**	**-2.143**	**0.032**
Year 2017	-0.567	0.443	-1.279	0.201
Year 2018	-0.459	0.418	-1.098	0.272
Year 2019	**-1.002**	**0.413**	**-2.428**	**0.015**
Snow duration	**0.558**	**0.118**	**4.713**	**0.000**
Biomass	**-0.766**	**0.114**	**-6.74**	**0.000**

Table 3.4 Demographic data recorded during live-trapping efforts from 20 June–13 August 2016 and the following year from 6 June–28 July 2017 within each region.

Region	Year	Unique captures	Recaptures	Total captures	Trapnights	Adult females	Leverets	Female: leveret[a]
NB	2016	38	33	71	1075	17	41	0.41
	2017	22	32	54	792	8	14	0.57
WMNF	2016	14	10	24	1550	7	9	0.78
	2017	6	6	12	434	4	0	-

[a] Number of adult females to leveret captures provides an index of reproductive output.

Table 3.5 Number (N) of mortality events of radio-collared snowshoe hares monitored from 21 June 2016–15 May 2018 within each region. The cause of mortality and predator were determined from evidence at the mortality site (see Text A2 in Appendix C).

Region	Sex	N	Cause of mortality	Predator	Notes
NB	F	4	Unknown	-	
NB	F	1	Predation	bobcat	
NB	F	1	Predation	coyote	
NB	F	2	Predation	mustelid	Likely a fisher
NB	F	1	Predation	terrestrial predator	Likely a larger predator (bobcat or coyote)
NB	F	10	Predation	unknown	
NB	M	12	Unknown	-	
NB	M	2	Predation	avian predator	
NB	M	1	Predation	coyote	
NB	M	1	Predation	fisher	
NB	M	5	Predation	unknown	
WMNF	F	1	Unknown	-	
WMNF	F	1	Predation	canid	
WMNF	F	1	Predation	mustelid	Likely a marten
WMNF	M	1	Unknown	-	
WMNF	M	1	Predation	unknown	Likely an avian predator
WMNF	M	1	Predation	fisher	
WMNF	M	1	Predation	marten	

Figure 3.1 Location of study areas for evaluating snowshoe hare (*Lepus americanus*) demography in the northeastern U.S. Remote cameras (*n* = 257) were used for evaluating distribution dynamics (upper left) and the CL, NB, and WMNF regions were used for evaluating density, population fluctuations, survival, and reproduction. The rectangular stands (*n* = 60) in the CL, NB, and WMNF were used for estimating relative density via the pellet-plot method and the white outlined grids (8 x 8 km) in the NB and WMNF are the locations of the telemetry study.

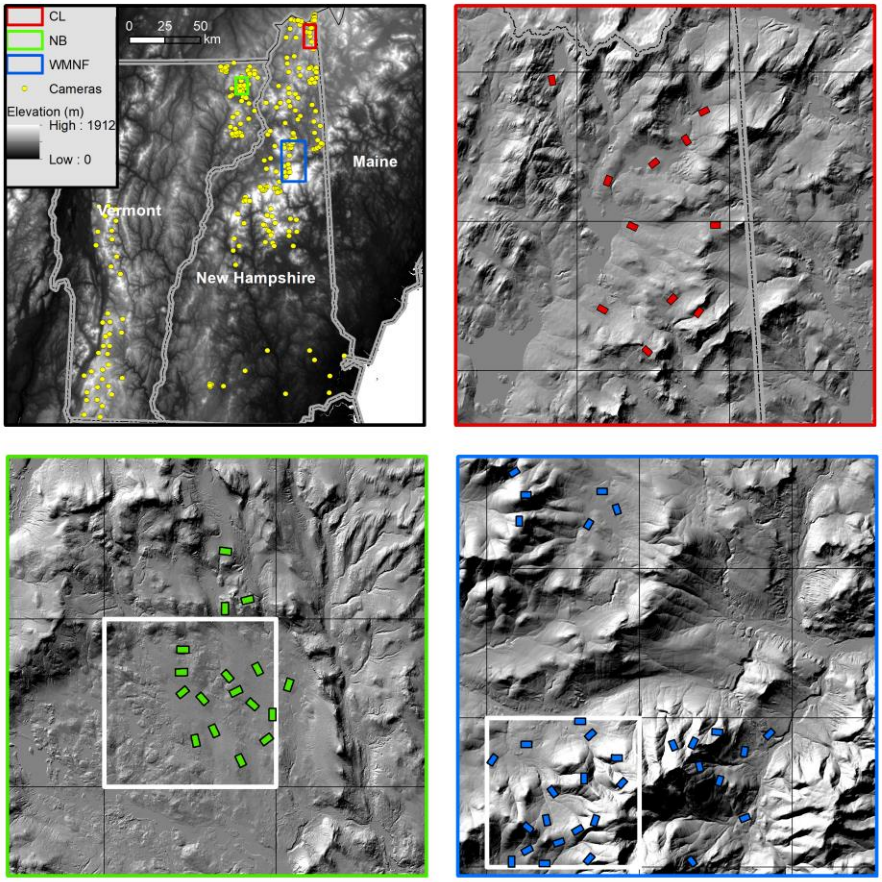


Figure 3.2 Duration of snow cover (A) and biomass (B) were the top abiotic and biotic predictors (respectively) of snowshoe hare occupancy using camera survey data collected from 2014 to 2019 in the U.S. states of New Hampshire and Vermont. Covariates not included in the plot were held at their mean value (i.e., biomass was held at its mean for A and snow cover was held at its mean for B).

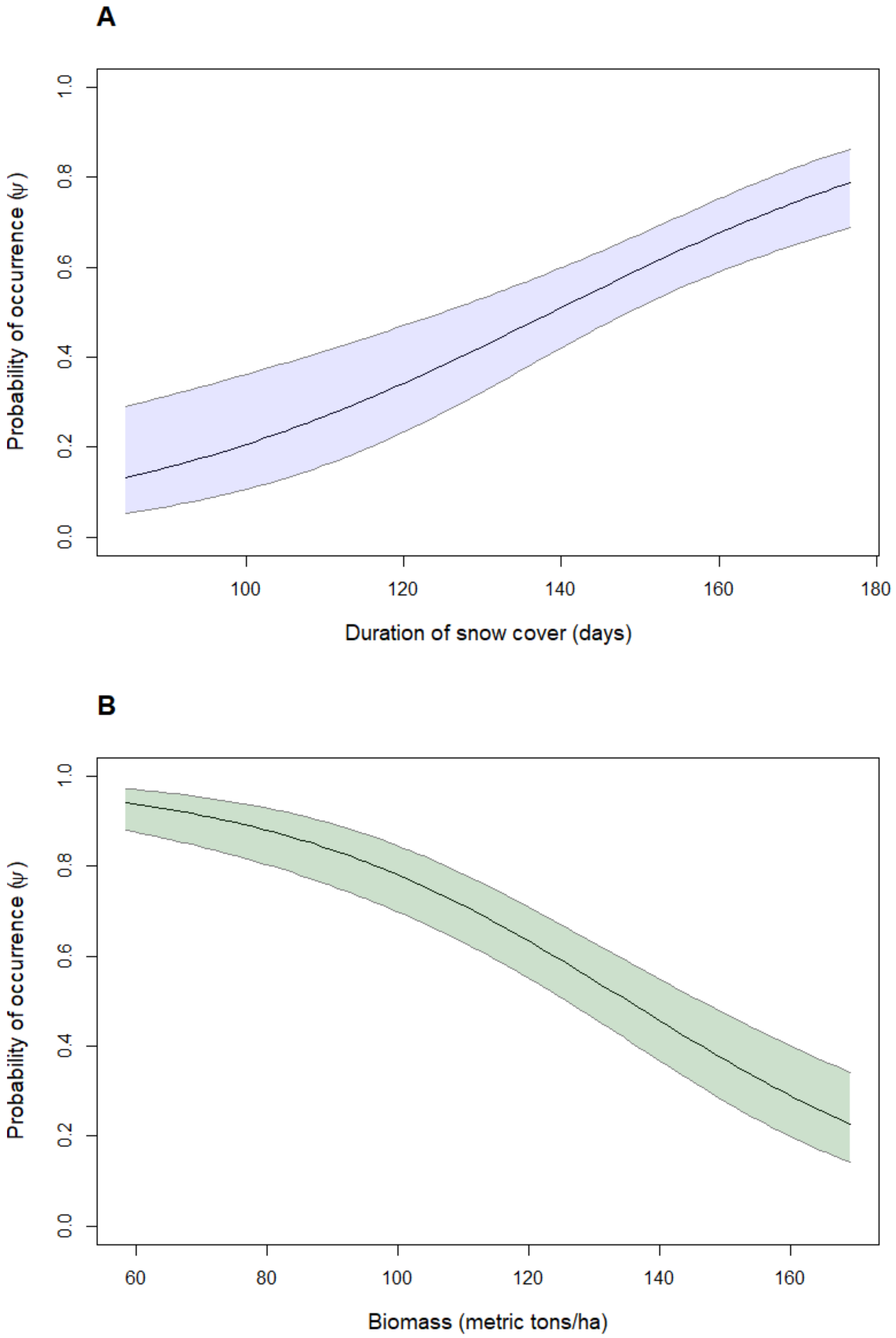


Figure 3.3 Differences in relative hare density (pellets/m^2/day) for 6 forest types in the NB, CL, and WMNF and differences between regions (inset), using pellet data collected from 2015–2019. Note, the error bars are not visible for late hardwood stands due to infinitesimal confidence intervals.

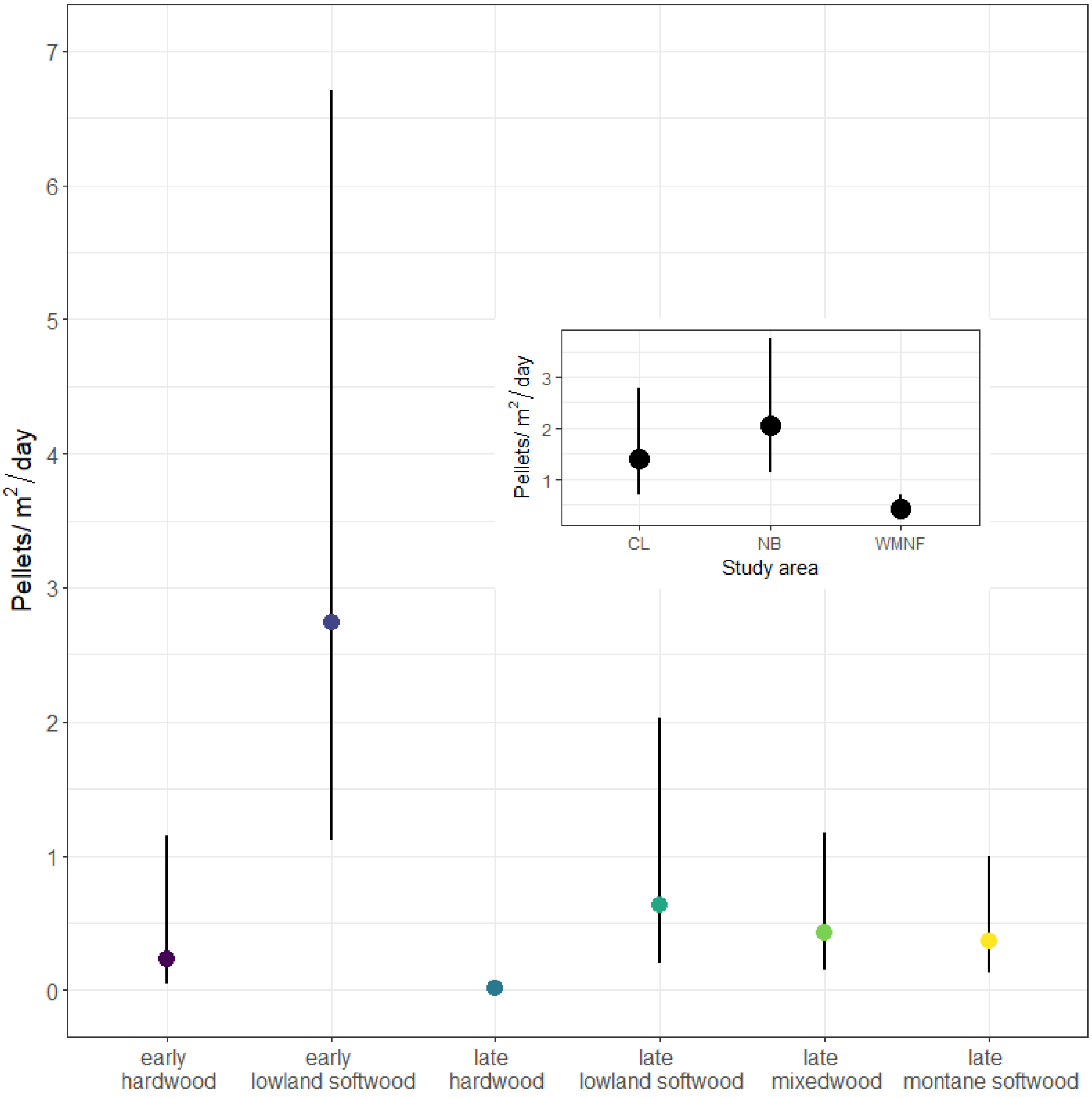


Figure 3.4 Annual variation in relative hare density (pellets/m^2/day) in the CL, NB, and WMNF regions from 2015–2019 as indexed using data from pellet surveys.

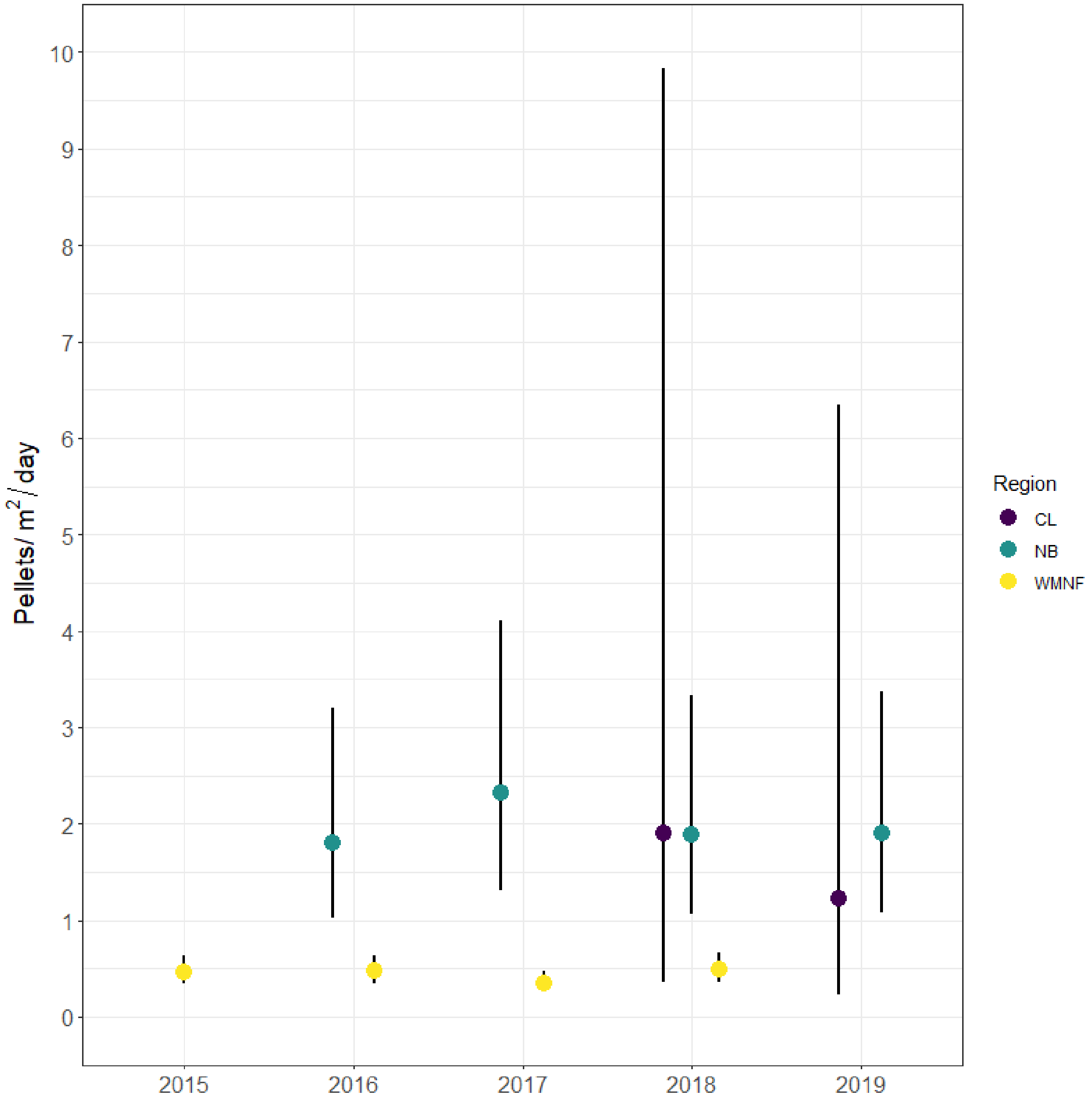
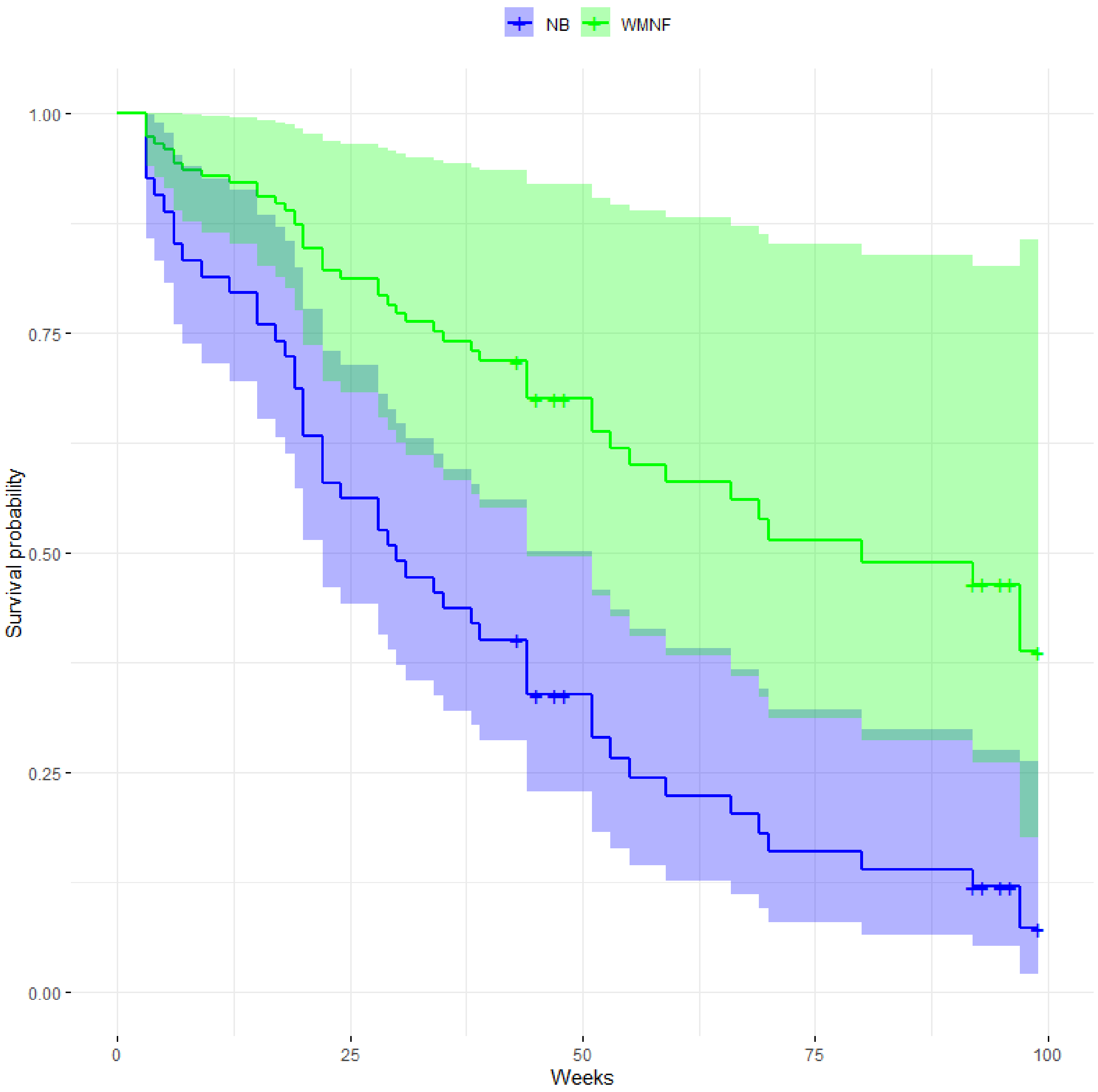


Figure 3.5 Comparison of weekly survival between the NB and WMNF regions over a 100-week period using 62 animals (NB = 48 hares; WMNF = 14 hares). Fifteen hares (NB = 9; WMNF = 7) remained at the end of the study period.



CHAPTER 4

FORECASTING SPECIES DISTRIBUTIONS: CORRELATION DOES NOT EQUAL CAUSATION

4.1 Introduction

A variety of extrinsic and intrinsic factors influence a species' distribution, including climate, biotic constraints, demographic limitations, and evolutionary adaptations (Connallon & Sgrò, 2018; Sexton et al., 2009), with varying degrees of influence on upper and lower range limits (Louthan et al., 2015; Sirén & Morelli, 2019). Recent research has focused more on understanding correlative relationships with a strong leaning towards the role of abiotic factors on the formation of geographic ranges (i.e., a species fundamental niche; Sexton et al., 2009) due to the increasing threat of climate change. However, without an understanding of the causal mechanisms that determine species distributions and range limits, the ability of correlative predictions to characterize current or future distribution dynamics is unclear (Filazzola, Matter, & Roland, 2020; Lyons & Kozak, 2019). Given the unprecedented rate of climate and habitat change, it is critical to understand the determinants of range limits to accurately predict future species distributions.

The concurrent development of new theory (Godsoe, Franklin, et al., 2017; Sirén & Morelli, 2019), statistical approaches (Lefcheck, 2016), and field methods (Sirén et al., 2018; Steenweg et al., 2017) provides a unique opportunity to evaluate the causal mechanisms that form species range limits. For example, a combination of direct and indirect abiotic and biotic forces has been shown to shape the range limits of North

American carnivore assemblages (Sirén et al., In Review), with snow having a strong indirect effect on the distribution of Canada lynx (*Lynx canadensis*) by mediating the negative effects of its competitors, primarily the closely-related bobcat (*Lynx rufus*). Although previous work has identified the importance of snow for many boreal forest mammals along trailing edges (Aubry, McKelvey, & Copeland, 2007; Jensen & Humphries, 2019; Peers et al., 2013; Sultaire, Pauli, Martin, Meyer, Notaro, et al., 2016), correlational approaches have precluded identification of the underlying mechanisms. Given that quantifying biotic and abiotic relationships is central to predicting future species distributions under climate change, an obvious and important question that emerges is whether predictions of current and future patterns are consistent when contrasting correlative and causative analytical frameworks.

In this paper we used realized relationships from causal and correlational models to predict current (2014–2019) and future (2080) distributions of Canada lynx and bobcats given projected changes in climate and habitat availability under a high greenhouse gas emission scenario (RCP8.5). We hypothesized that the inclusion of direct and indirect effects, via a causal modeling framework, would provide more accurate distributions than correlative models. Accordingly, we predicted that the mediating effect of snow depth on biotic interactions (e.g., competition) and bottom-up effects from habitat availability, as modeled using a causal approach, would more accurately depict species' ranges during the current period than a correlative framework. Following this logic, we hypothesized that causal and correlative frameworks would predict different effects of the projected changes in snowpack and biomass on future species' distributions. Our prediction was that causal models would propagate these changes less extremely than correlative models due to the inclusion of biotic interactions.

4.2 Methods

4.2.1 Study system

Sirén et al. (In Review) describe a causal system that includes the direct and indirect effects of snow and forest biomass on two competing carnivores (Canada lynx and bobcat). This system, investigated through a large scale 6-year camera trapping effort across the U.S. states of Vermont and New Hampshire (Fig. 4.1, Fig. A1 in Appendix D), presents a unique and timely opportunity to compare causal and correlative predictions of current and future predictions of species distributions of the lynx, a species of conservation interest, and its closely-related competitor, the bobcat, which negatively influences occurrence probability (Sirén et al., In Review).

4.2.2 Modeling approach

We analyzed camera trap data using causal and correlative frameworks to predict current and future distributions of lynx and bobcats across their range in the northeastern U.S. For correlative predictions, we fit a single-season, single-species occupancy model (MacKenzie et al., 2017) with snow depth and forest biomass as predictor variables. For the causal model we used structural equation modeling (SEM) (Lefcheck, 2016) and a modification of the causal system described in Sirén et al. (In Review) that only included snow depth and forest biomass as exogenous variables and bobcat as a competitor of lynx. For an overview of SEM, see Text A1 in Appendix B. We chose a simplified causal system, without prey species, to provide a fair comparison with the correlative model.

Note that for the SEM, we used ‘detection corrected’ occupancy estimates from an occupancy model with a null state model and maximal detection model (Duclos et al., 2019; Sirén et al., In Review).

Predictions and uncertainty (standard errors) under the correlative occupancy modeling framework are straightforward as current and future landscape patterns can be predicted directly using standard GLM-like prediction routines. The conditional structure of the SEM, on the other hand, requires a sequential bootstrapping approach, where realizations of each model in the conditional hierarchy of the SEM are simulated and included in the next sub-model. Operationally, this required simulating spatially explicit bobcat occupancy states from the bobcat model and carrying those over into the lynx model and repeating 1,000 times. We calculated standard errors from these simulations to map uncertainty in realized occupancy. We then used each model to make two sets of landscape predictions of occupancy for lynx and bobcats: one for the current period (2014–2019) and one for the future (2080) using snow depth and forest biomass as predictor/exogenous variables.

4.2.3 Snow and forest biomass data

We used gridded snow depth and forest biomass datasets (Duveneck & Thompson, 2019; Wang, Hamann, Spittlehouse, & Carroll, 2016) that included current and future projections of these variables under a high carbon emission scenario (representative concentration pathway [RCP] of 8.5 W/m^2; hereafter, RCP8.5) to model species distributions. We used ClimateNA software (Wang et al., 2016) to obtain outputs of snow depth (precipitation as snow; mm). To match the resolution of the forest biomass data, we downscaled all snow data to 250 m using a resampled digital elevation model (original resolution was 90 m) obtained online through the National Map Program ("The National Map - Data Delivery,"). We downloaded snow data for the current period and selected data from the HadGEM2-ES global circulation model (GCM) for the future period. We chose this GCM because, compared to other GCMs, it best reproduces winter precipitation patterns for the northeastern U.S. (Karmalkar, Thibeault, Bryan, & Seth, 2019). We used a regional forest biomass (kg/m^2) model (250 m spatial resolution) for the current and future periods that incorporated climate and land use change under RCP8.5 (Duveneck & Thompson, 2019). Although this model only projected changes in biomass until 2060, we assumed that differences between 2060 and 2080 would be marginal compared to changes in snow.

4.2.4 Model performance

To evaluate the predictive ability of causal and correlational models from the current period, we compared spatial predictions with independent data. We used snow track survey data collected during the same time period and region as our primary independent data source (Fig. A2 in Appendix D). Briefly, we conducted snow track surveys along established routes 1–3 times/winter following a protocol used to detect mesocarnivores (Squires, Olson, Turner, Decesare, & Kolbe, 2012). All track intercepts of lynx and bobcat were recorded with a GPS (Garmin GPS 62S, Garmin International, Olathe, KS, USA) and detections/non-detections were spatially assigned to a 2x2 km grid (Fig. A2 in Appendix D). In total, we used 50 detections of lynx and 73 detections of bobcats from 91 surveys over a 6-year period to validate the causal and correlative occupancy models. Because snow track surveys only encompassed a portion of the area we sampled with cameras (see Fig. A2 in Appendix D), we assigned lynx occurrence records collected by state agencies (New Hampshire, Vermont) during the same timeframe to the grids. Given that lynx is a federally-listed species and both states have been surveying them extensively over the past decade, we assumed lynx were absent for any grid without an occurrence record. We did not have this information for bobcats, so we could not make this assumption. Therefore, we only evaluated model performance of bobcats in the snow track survey region. We used the area under the receiver operating characteristic curve (AUC) to evaluate the performance of each model to predict occurrence; models with AUC values between 0.5 and 0.7 are considered to have low accuracy, those between 0.7 and 0.9 are considered adequate at predicting occurrence and those with values >0.9 are deemed highly accurate (Manel, Williams, & Ormerod, 2001). Finally, to evaluate differences in spatial predictions (and uncertainty of the predictions), we visually inspected differences between modeling approaches and periods.

All analyses were conducted using R statistical software (R Core Team, 2019); for a complete list of the packages, see Table A1 in Appendix D.

4.3 Results

4.3.1 Model inference

The causal model fit the data well (Fisher's $C = 0.512$, $P = 0.774$), indicating conditional separation, which is a core assumption of SEM. This model explained 4% and 39% of the variation in lynx and bobcat occurrence, respectively (Fig. 4.2A).

Lynx occupancy, evaluated using a causal framework, was influenced by a combination of abiotic and biotic factors. Snow depth had a direct and indirect positive effect on lynx occupancy, the latter realized via a path through bobcats (Table 4.1, Fig.

4.2A). Specifically, snow depth had a direct negative effect on bobcat occupancy and bobcats had a direct negative effect on lynx occupancy (Fig. 4.2A). Forest biomass also had a negative effect on lynx occupancy; lynx were more likely to occur in areas with lower forest biomass (Table 4.1, Fig. 4.2A).

For correlative models, lynx occupancy was positively correlated with snow depth and negatively correlated with forest biomass (Table 4.1, Fig. 4.2B, Fig. 4.3). Bobcat occupancy, on the other hand, was negatively correlated with snow depth, whereas biomass had a weak positive effect (Table 4.1, Fig. 4.2B, Fig. 4.3).

4.3.2 Model performance

We evaluated the predictive ability of causal and correlative models using independent data collected in the same region and time period as our camera data. The predictive performance, as measured using the area under the receiver operating characteristic curve (AUC), revealed that the causal model was better at predicting occurrence (AUC = 0.92) than the occupancy model (AUC = 0.86; Fig. A3 in Appendix D). The predictive performance of all bobcat models had marginal accuracy (AUC = 0.66–0.68; Fig. A4 in Appendix D). Consequently, we only compared differences between the causal and occupancy models for lynx except to interpret the effect that bobcats had on lynx.

4.3.3 Model differences for the current period

Predictions for lynx distribution during the current period (2014–2019) under the causal modeling framework were similar to the correlative model, but there were some notable differences (Fig. 4.4). For both models, predicted occupancy (and uncertainty) was highest in the northeastern and high elevation areas of the region (Fig. 4.4, Fig. A5 in Appendix D). However, the correlative model also predicted high lynx occupancy in areas where they do not occur (e.g., western, and southeastern regions; Fig. 4.4). Contrastingly, the causal model predicted these regions to have low occurrence due to high predicted occurrence of bobcats in this region (Fig. 4.4).

4.3.4 Model differences for the future (2080)

For both modeling approaches, predicted distribution in the region changed under a high emissions scenario (Fig. 4.4). Both models predicted an increase in occupancy for lynx in the northeastern part of the region (Fig. 4.4), although with less precision compared to other areas (Fig. A5 in Appendix D). However, the causal model predicted a relatively lower increase compared to the correlative model (Fig. 4.4). Lynx occupancy, as predicted by the correlative model, was predicted to increase in areas they were unlikely to exist in the current period (e.g., western region; Fig. 4.4). Although the causal model predicted a slight increase in these regions, predicted occupancy was already low in both periods due to high predicted occurrence of bobcats (Fig. 4.4). Both modeling approaches predicted an overall decline in occupancy for lynx in the high elevation regions, except for the highest elevations. However, the causal model predicted a slightly greater decrease (Fig. 4.4) due to an increase in predicted bobcat occupancy during the future period (Fig. 4.4).

4.4 Discussion

There is overwhelming evidence that climate and land use change alter species' ranges even within relatively short time frames (Sirén & Morelli, 2019). However, the interactive nature of these factors and their influence on biotic interactions has been largely unexplored. We interrogated the theory that climate mediates competition between species along distributional edges (Sirén & Morelli, 2019) using a causal modeling framework. Our comparison with correlative models indicates strong support for taking a systems approach that allows for the inclusion of direct and indirect effects to predict current and future distributions. We discuss our findings within the context of ongoing global change and implications for modeling species distributions.

The causal lynx occupancy model that incorporated climate-mediated competition between the phylogenetically similar bobcat had higher predictive power than the correlative one. These findings uphold previous work that suspected this dynamic (Hoving et al., 2005; Peers et al., 2013; Scully et al., 2018), yet could not rule out alternative hypotheses due to the use of correlative frameworks. Although the correlative model predicted lynx occurrence in similar regions, it also predicted occurrence in areas where lynx do not occur (e.g. western Vermont, southeastern New Hampshire). These regions are highly developed (e.g., agriculture) with low forest biomass and shallow snow. Because biomass had a stronger effect than snow depth on lynx occurrence, according to the correlative model, these regions were predicted to have high lynx occurrence. However, these regions were also predicted to have high bobcat occurrence because of shallow snow depth. Using a causal modeling framework, we were able to explicitly incorporate these interactions and the model accurately predicted low occupancy in these regions.

As hypothesized, the similarities and differences in lynx occupancy during the current period, as predicted using causal and correlative models, were propagated into the future. Both modeling approaches revealed that lynx occupancy declined at high elevation in the central region and increased in the northeast. However, as predicted, the changes highlighted by the causal model were less extreme than the correlative model. Further, the correlative model predicted a marked increase in the western region likely due to projected human development in southern New England that reduces forest biomass (Duveneck & Thompson, 2019). The causal model, which predicted low occurrence in this region during the current period, also predicted a slight increase in this region. However, given that bobcats were also predicted to increase, this muted the response. A more likely scenario is the increase in lynx occupancy in the northeastern region which, despite having lower snow, is projected to have more early-successional habitat due to large-scale forest management (Duveneck & Thompson, 2019). These findings are consistent with previous work that highlights the influence of land management on lynx expansion in the region (Simons-Legaard et al., 2016).

Of note, our previous modeling work indicated that forest biomass had a weak direct effect on lynx occupancy (Sirén et al., In Review). Forests with low biomass (i.e., early regenerating forest) have strong bottom-up effects on the preferred prey of lynx – snowshoe hares (*Lepus americanus*) (Sirén et al., In Review). Our causal model only included a direct effect of biomass, so the strong relationship we observed suggests that biomass was likely a proxy for prey availability. However, given that we used different sources of forest biomass, some differences are expected between this paper and our previous work (Sirén et al., In Review). These differences, though, do point towards the need to evaluate a range of gridded data products. Because we were limited by the availability of current and future projections of biomass, this constrained the number of scenarios we could evaluate.

We explored a new approach to predicting species distributions using a causal modeling approach that incorporated direct and indirect effects. Although this approach provided a more accurate representation of the lynx range, there were limitations. Thus, we only evaluated a simple causal model to make comparisons with the correlative one. The propagation of errors will only increase as the complexity of the model increases and how to deal with this uncertainty is unresolved (J. Lefcheck, email communication). Ideally, a more thorough examination of how these errors move through a causal model to influence predictions will be useful. Moreover, we only used a simple additive correlative model for comparison. Other correlative approaches, e.g., a multi-species occupancy model, might provide similar outputs to the causal model (e.g., Rota et al., 2016). Finally, adopting a causal framework requires learning a new statistical paradigm (i.e., SEM), which may limit the utility of this approach for modeling species distributions.

Regardless of these uncertainties, our paper represents the first, hopefully of many, species distribution model that uses a causal framework. Most importantly, though, we were able to show how climate mediates competition between alike species. These findings can be used to guide management and conservation decisions for Canada lynx and other winter-adapted species along trailing edges that are predicted to decline due to climate change (Aubry et al., 2007; Carroll, 2007; Sultaire, Pauli, Martin, Meyer, Notaro, et al., 2016).

Table 4.1 Effects (standard errors) of predictors on species' occupancy for causal and correlative models.

Statistical Approach	Predictor variable	**Canada lynx** (*Lynx canadensis*)	**bobcat** (*Lynx rufus*)
Correlative	Snow depth	1.090 (0.215)***	-1.520 (0.261)***
	Biomass	-1.54 (0.242)***	0.327 (0.192)
Causal	Snow depth	0.413 (0.104)***	-1.200 (0.244)***
	Biomass	-0.295 (0.099)**	-
	Bobcat	-0.629 (0.299)*	-

Asterisks indicate significance level (**P* <0.05, ** *P* <0.01, *** *P* <0.001)

Figure 4.1 Current (2010) and projected snow depth (mm) for 2080 and forest biomass (kg/m^2) for 2060 given a high-emissions scenario (RCP8.5) in the northeastern U.S. Species occurrence data for causal and correlational models were collected over a six-year period (2014–2019) using 257 remote cameras (white dots; upper left) that were distributed along latitudinal and altitudinal gradients.

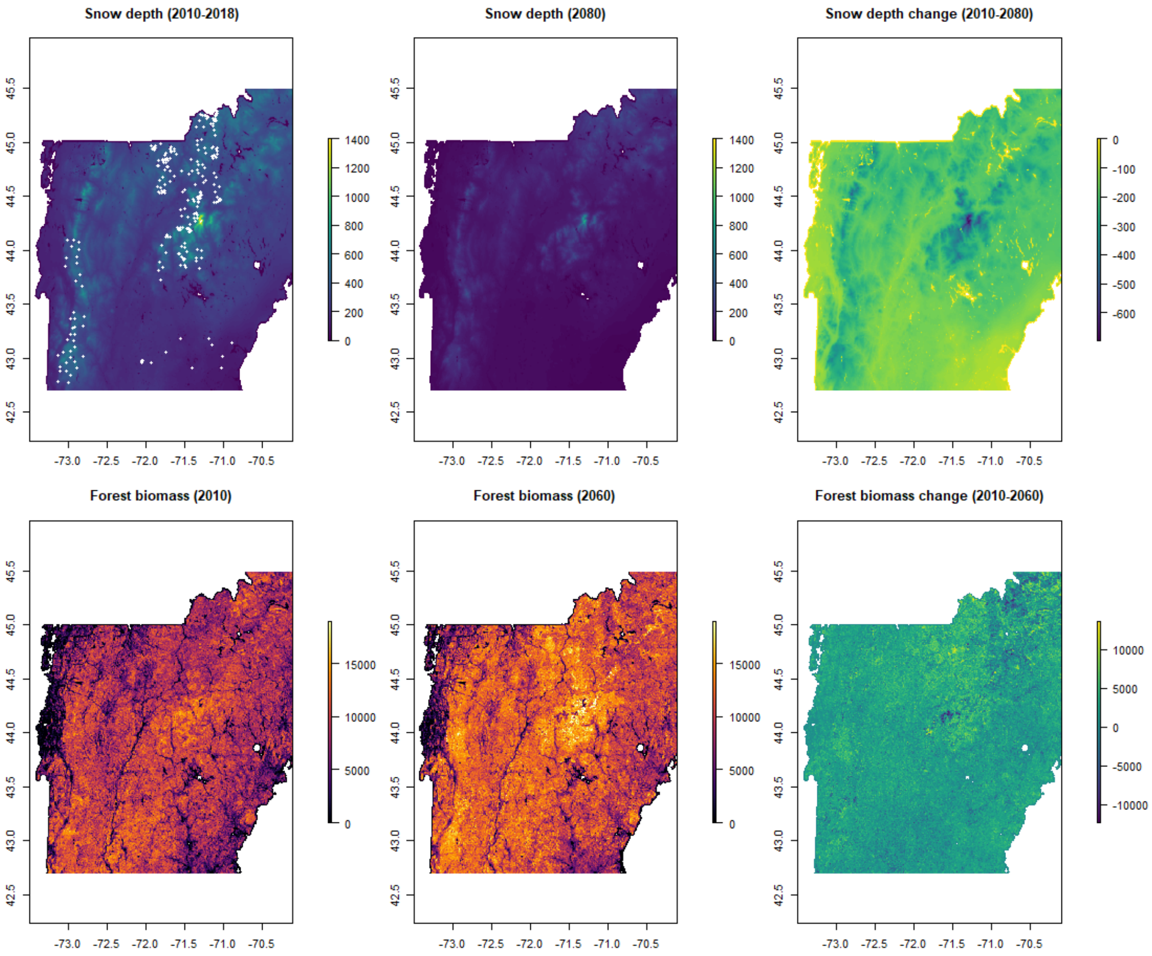


Figure 4.2 Causal model (A) evaluating the direct and indirect effects of snow depth (mm) and forest biomass (kg/m^2) on bobcat (*Lynx rufus*) and Canada lynx (*Lynx canadensis*) occurrence and the direct effect of bobcats on lynx. Solid and unidirectional arrows represent direct effects and dashed bidirectional arrows signify correlated errors among variables. Superscript symbols indicate significance level (*P <0.05, ** P <0.01, *** P <0.001) and conditional R^2 values (% of variation explained by the fixed and random effects) are listed within respective nodes. Correlative model (B) evaluating the direct effect of snow depth and forest biomass on lynx and bobcat occurrence. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols).

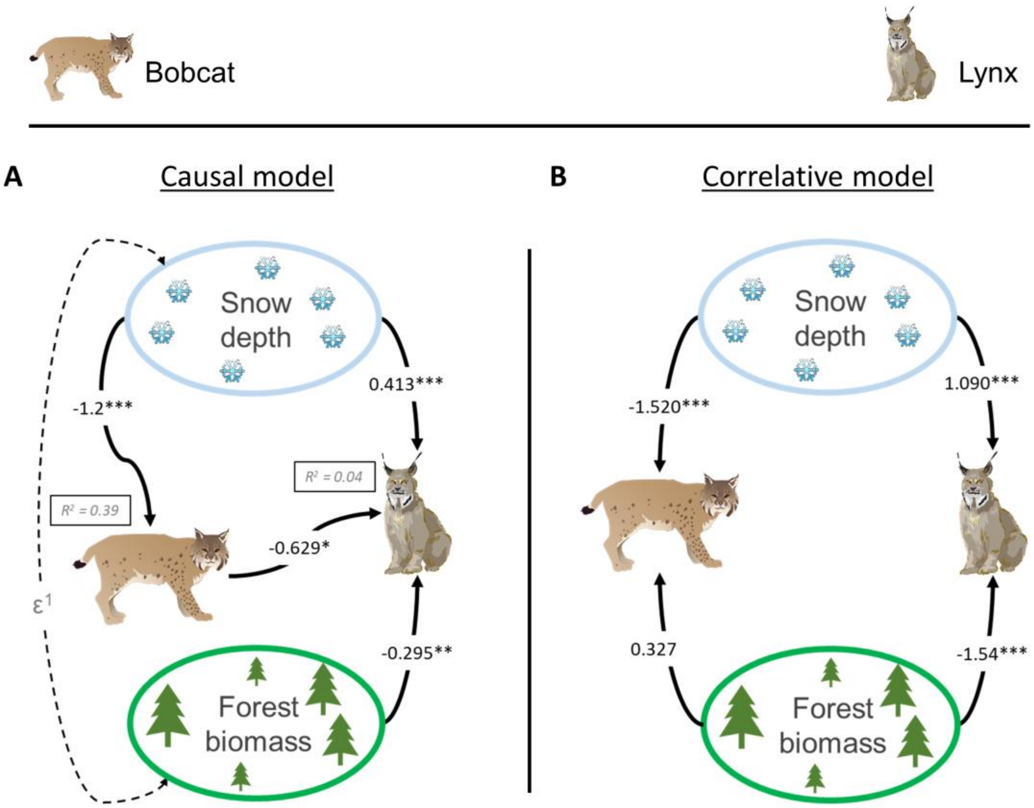


Figure 4.3 Influence of snow depth and forest biomass on bobcat (*Lynx rufus*) and Canada lynx (*Lynx canadensis*) occupancy using camera survey data collected from 2014 to 2019 in the U.S. states of New Hampshire and Vermont.

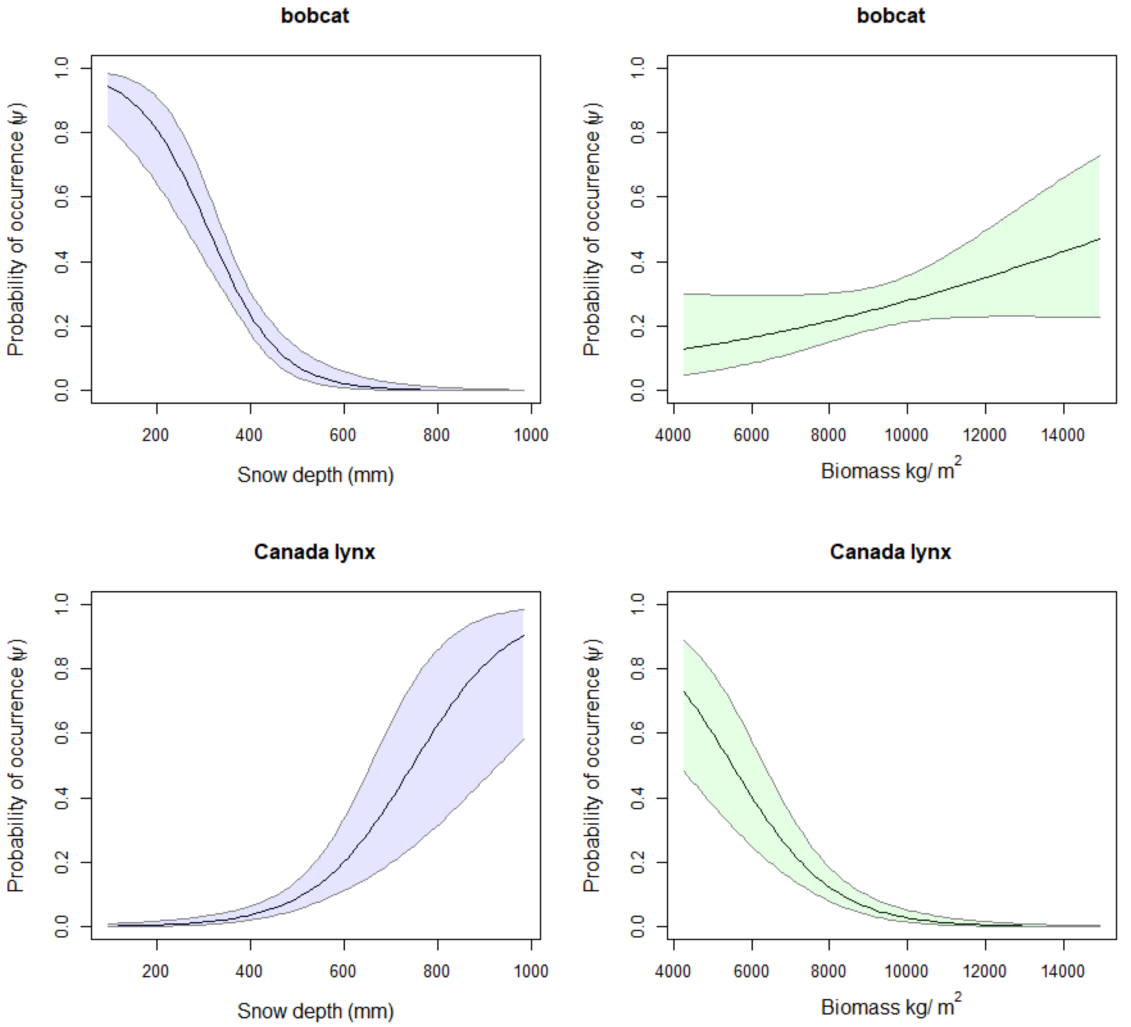
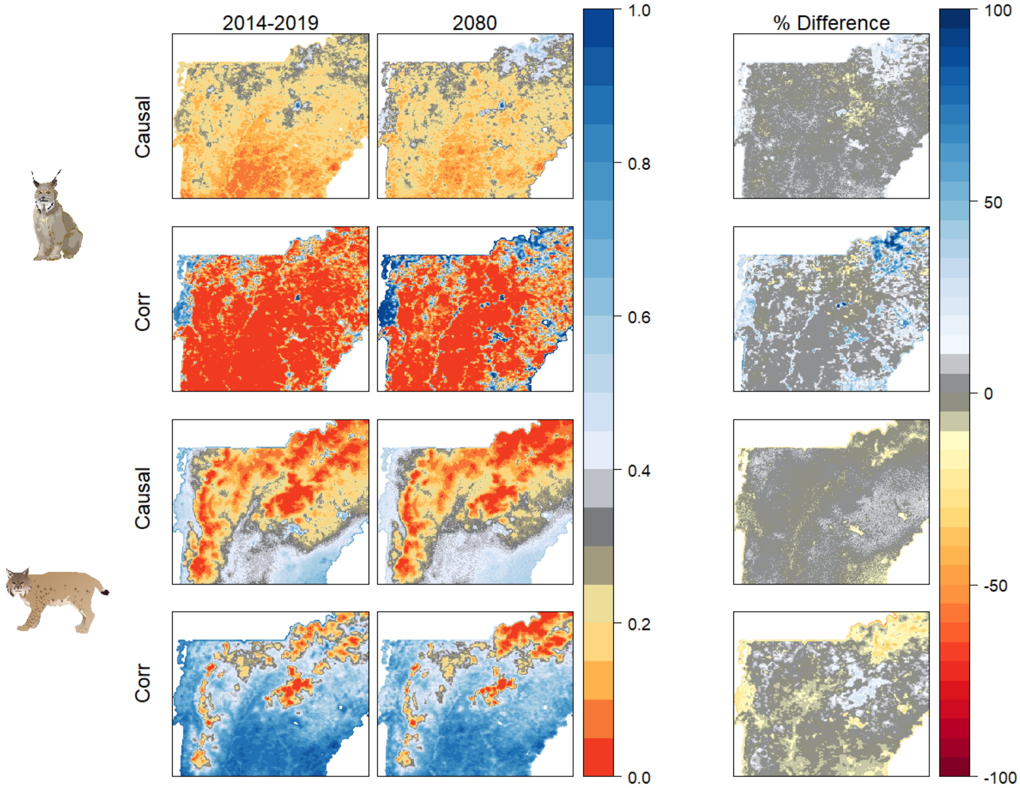


Figure 4.4 Canada lynx (*Lynx canadensis*) and bobcat (*Lynx rufus*) distributions, as predicted using causal and correlative (corr) models for the current period (2014–2019) and the future (2080) given projected changes in snow depth (mm) and forest biomass (kg/m^2) in the northeastern U.S. The third column indicates % difference in distributions between the current and future periods. Positive differences indicate an increase in occupancy and negative values indicate a decrease.



CHAPTER 5

CONCLUDING REMARKS

5.1 Introduction

The overarching pursuit of my dissertation was to advance theoretical and empirical understanding of factors that limits species' ranges. A major knowledge gap in biogeography and ecology is the role of biotic interactions on range limits. Although previous work, dating all the way back to Charles Darwin, indicates that biotic interactions can limit species' ranges, especially along equatorial edges, there is more empirical support for climate as a limiting factor. In my dissertation, I developed a theoretical framework and provided the empirical support to address this knowledge gap. The primary motivation of addressing this theory was to better understand the impacts of climate and land use change to conserve threatened and endangered populations. Because we are in the midst of one of the greatest conservation crises, and arguably the greatest environmental crisis, that humanity has ever seen, the impetus to make a difference was at the forefront of my mind. I sincerely hope that my dissertation extends beyond the walls of academia to inform conservation decisions and encourage policy-makers to prioritize ecological perspectives in addressing climate change.

For my first chapter, I revisited the theory, first proposed by Charles Darwin (1859), that abiotic stress forms upper distributional limits and biotic interactions causes lower limits (range-limit theory; RLT). I proposed an expansion to RLT, interactive RLT (iRLT), to understand the causes of range limits and predict shifts. From an integrative review of North American mammalian carnivores and herbivores, I found that range limits are more nuanced and interactive than predicted by RLT. Many studies (57 of 70) indicated that biotic factors can ameliorate harsh climate along upper latitudinal/altitudinal limits whereas climate stress can mediate biotic interactions along lower limits (44 of 68 studies). These secondary, and often indirect, effects facilitate range expansion, contraction or stability depending on the strength and the direction of the abiotic or biotic factors. In support of RLT, biotic interactions most often occurred along lower limits, yet, as predicted by iRLT, there were notable trophic differences. Carnivores were only limited by competitive interactions (n = 25), whereas herbivores were more influenced by predation and parasitism (55 of 71 studies); these trophic differences led to divergent range patterns along lower limits. This dissertation chapter provided the theoretical framework for my research and highlighted unifying patterns of previous research on North American mammals. This review also indicated that iRLT extends to other taxa and biomes outside of North America. As such, I advocate using iRLT to understand current distributions and as a heuristic model to predict how and where species' ranges will shift in the future. In the face of global change, iRLT provides a mechanistic framework for disentangling the causes of range limits to make effective conservation and management decisions.

For Chapter 2, I evaluated the two primary hypotheses of iRLT using occurrence data of carnivore and prey populations along upper and lower range limits in the northeastern U.S. I found that snow directly limits populations at high altitudes and higher latitudes, but prey or habitat availability can influence range dynamics, supporting my first hypothesis. For example, bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) were limited by deep snow and long winters along upper edges but the availability of an abundant prey base, including temperate and boreal species, had a strong positive effect, especially for bobcats. Conversely, snow had a strong positive effect on the lower limits of Canada lynx (*Lynx canadensis*) and American martens (*Martes americana*). For lynx, the indirect effect of snow was strongest and countered the negative effect of competition, especially between the phylogenetically similar bobcat, providing support of my second hypothesis that climate mediates competition between similar species and forms lower range limits. Further, prey and habitat availability had strong direct and indirect effects for lynx and martens, indicating that several factors are important for populations along lower limits. This chapter supports iRLT and underscores the need to consider direct and indirect mechanisms for studying range dynamics and species' responses to global change.

To further evaluate iRLT, I studied the influence of climate and resource availability on snowshoe hare (*Lepus americanus*) – one of the most ecologically important herbivores of boreal and sub-boreal forests – along its trailing edge in North America. For Chapter 3, I collected data on distribution, population density and fluctuations, habitat use, survival, and reproduction to test the hypothesis that density dependence determines, in part, species' persistence along trailing edges. From a 6-year study (2014–2019), I found that variability in snow and resource availability affects density and population fluctuations and leads to trade-offs in survival and reproduction for snowshoe hare populations in the northeastern U.S. Hares living in resource-poor environments had lower and stable population density, lower reproductive effort, yet higher survival compared to populations living in resource-rich environments. I suggest that density-dependent dynamics, elicited by resource availability, provide hares a unique survival advantage and partly explains persistence along their trailing edge. I hypothesize that this low-density escape from predation and parasitism occurs for other prey species along trailing edges, but the extent to which it occurs is conditional on the quality of matrix habitat. Given that species ranges are shaped by several factors other than climate, including biotic and intraspecific factors, I advocated for a more careful examination of factors influencing populations along trailing edges to better inform conservation and management decisions.

For Chapter 4, I evaluated the predictive ability of iRLT by comparing a causal model (the quantitative framework of iRLT) with a correlative occupancy model. I compared current (2014–2019) and future (2080) distributions of Canada lynx along its lower range limit in the northeastern U.S. under a high-emission scenario (RCP8.5) of projected snow and forest biomass change. My hypothesis that climate-mediated competition, exemplified by causal models, would result in different distributions than correlational models, both in the current and future periods was well-supported. The causal model predicted the current distribution of lynx more accurately because it incorporated the influence of competitive interactions mediated by snow with the closely related bobcat. Both modeling frameworks predicted an overall decline in occupancy in the central high elevation regions and increased occupancy in the northern region due to changes in land use that provided optimal habitat. However, these losses and gains were tempered by the inclusion of indirect and direct effects from causal model. This comparative analysis of my dissertation indicates that a causal framework, steeped in ecological theory, should be used to predict species' response to global change.

Although not a central theme of my dissertation work, I developed a novel camera trap method that allows for the simultaneous collection of snowpack and species occurrence data (Sirén et al., 2018). I used occurrence data from this field method to evaluate my theory on range limits and I used camera observations of snow depth to evaluate bias in a gridded snow data product that is commonly used by ecologists to investigate the influence of snow on wildlife populations. Over a 6-year period, I collected over 150,000 observations of snow depth from 257 cameras. I found that commonly used gridded snow data consistently under-predicted snow depth, especially at high elevation regions. Data from this field method can be used to bias-correct gridded snow data to provide more accurate assessments of climate-wildlife dynamics but also be used by climate scientists to improve the accuracy of current models and those that project snow at future periods given ongoing and plausible carbon emission scenarios.

Overall, my dissertation has advanced biogeographical and ecological theory on range limits. The primary contributions are: 1) Climate mediates biotic interactions along lower range limits. 2) Bottom-up factors have strong influence on upper but also lower limits. 3) Biotic interactions vary by trophic level and have divergent effects along lower limits. These contributions have clear implications for wildlife conservation and management, especially for populations along lower limits that are likely most vulnerable to climate change. Results from my dissertation have already been used to inform listing decisions for the federally-threatened Canada lynx and to conserve land for state-endangered species such as American marten. Further, my finding that neutral matrix habitat provides snowshoe hares a low-density refuge from predation along its lower limit is contrary to previous work. Although this finding warrants more examination, it suggests there are several approaches for sustaining populations along trailing edges. Finally, my finding that distribution models developed using an iRLT framework have higher predictive power than correlative models provides strong evidence for including direct and indirect effects in species distribution models. This dissertation fills fundamental gaps in understanding causes of range limits and provides new insight into how this affects carnivores and herbivores differentially.

APPENDIX A

SUPPLEMENTAL: INTERACTIVE RANGE-LIMIT THEORY (IRLT): AN EXTENSION FOR PREDICTING RANGE SHIFTS

Text A1.

To evaluate the degree of support for interactive range-limit theory (iRLT) – an extension of range-limit theory (RLT) – and the extent to which biotic interactions varied by trophic level, we performed a literature review of terrestrial and arboreal mammals from North America with an initial criterion of 30 genera from 10 families, representing 5 orders (Table S1). We chose genera as the finest taxonomic resolution because most studies included the genus name of a focal species, rather than higher taxonomic levels. We opportunistically included genera when our search results provided studies that were within the focus of the review, yet not included on the original list. We noted the occurrence of these genera in the text and tables below.

We used 2 approaches to search for literature. We used a systematic approach conducting 5 unique searches on the Web of Science (WOS) and 2 on Google Scholar (GS), using the same search terms for those that overlapped (Table S2). Note that GS has a 256-character limit and only provides the first 1,000 results so we performed multiple GS searches for each unique search. We also took a non-systematic approach, searching for literature on taxa that we were more familiar with, including our own studies. This approach allowed us to increase our sample size and find local and regional studies that evaluated causal mechanisms influencing fitness along range edges. It also provided older literature that may have used terminology different than the search terms we used. We distinguished between systematic and non-systematic searches and summarized each.

From 23-31 January 2019, we performed two different searches based on the aforementioned criteria. Our first and second WOS searches provided a total of 63 and 11 results, respectively (Table S2). Our first and second GS searches provided a total of 6,620 and 1,758 results, respectively (Table S2). Our third – fifth searches from WOS provided a total of 358, 9, and 65 results, respectively (Table S2). From this list, we searched through each result, first examining the title and abstract to determine if the study met our criteria. For our first search, we obtained 33 and 112 relevant papers from WOS and GS, respectively. Our second search provided 3 and 34 relevant papers from WOS and GS, respectively (Table S2). We found 19, 4, and 22 relevant papers from our remaining WOS searches (Table S2). Note that GS typically provides more results as it does not filter out gray literature. Our combined search (taking overlap among and within searches and search engines into account) resulted in a total of 97 papers. We then split multi-species papers or those that evaluated dynamics along multiple edges (e.g., upper and lower elevation edges) into separate entries in order to evaluate each species separately. Combined, our systematic review provided a total of 135 entries that met our criteria. Our non-systematic review yielded 131 unique papers (154 after splitting multi-species papers into separate entries); of these, 33 of the papers overlapped with the systematic review. Accounting for multi-species studies, we narrowed our review to 342 entries from 257 unique papers.

To narrow our review further, we searched through each of the 342 papers and tallied multiple items, including the latitudinal/altitudinal edge (High-latitude/altitude, Low-latitude/altitude), ecological variable measured in the study (e.g., Distribution, Survival), abiotic factor (e.g., Temperature), biotic factor (e.g., Habitat), abiotic and biotic responses (Positive, Negative, Neutral, Inferred, NA), biotic interaction (Yes, Inferred, NA), biotic interaction type (e.g., Competition, Predation), whether or not the study was conducted beyond the limit of the species range (Yes/No), and the type of study (Observational, Experimental, Descriptive). Note, we recorded positive or negative abiotic or biotic responses if the study indicated a statistically significant effect; a neutral assignment indicated no statistical relationship. We also recorded if the study evaluated static or dynamic range edge dynamics, and if the latter we recorded if the population(s) expanded, contracted, or remained stable. Finally, we assigned the scale (Local, Regional, Geographic) of each study based on the following criteria. We characterized studies as “Local” if they only sampled one population or a subset of a population; these studies usually used methods such as radio-telemetry that are typically limited to local extents. We labeled studies as “Regional” if they sampled >1 population and/or used survey methods that allow for broad spatial sampling (e.g., camera surveys). Lastly, we characterized studies as “Geographical” if the authors explicitly noted that they surveyed the entire geographic range of a species; these studies often used museum or harvest data. To increase the accuracy of our classifications, we paid special attention to the text of each article to determine whether a study was “Local”, “Regional”, or “Geographic” and used these clues to further refine the scale of the study. Although, these definitions of scale may be somewhat arbitrary, these criteria allowed us to filter our results to ensure we were including studies that were appropriate for evaluating iRLT (i.e., we were not biasing results based on local patterns). We omitted any papers that were reviews (unless they also included a single-species case study) or not conducted along or near range limits. These final criteria reduced our list from 257 to 217 unique papers (342 to 290 entries, including papers with multi-species). These papers are listed below in the reference section. Our search from the systematic and non-systematic reviews increased the number of families and genera to 15 and 31, respectively, and provided a total of 52 species. We used these remaining studies to evaluate iRLT and the extent to which biotic interactions varied by trophic levels.

To evaluate support for iRLT, we selected studies that evaluated regional and geographic scale distribution (i.e., first and second order resource selection; sensu Johnson, 1980) or abundance; studies of abundance were rare and only represent a small proportion of our review. This reduced our list from 290 to 216 entries and excluded many of the local studies which evaluated measurements of fitness (e.g., survival); the latter entries were used to discuss the possible mechanisms limiting populations along range edges and evaluate the extent to which biotic interactions varied by trophic level. We filtered the distribution studies based on 2 criteria. Our primary method for evaluating iRLT included only those studies that evaluated abiotic *and* biotic factors (138 entries). Our secondary method only included studies that evaluated abiotic *or* biotic factors (78 entries). We evaluated evidence for iRLT based on 2 criteria: We expected that the original predictions of RLT would be evident (negative abiotic factors along high-latitude/altitude limits and negative biotic interactions along low-latitude/altitude limits), except for two caveats; studies of populations along high-latitude/altitude limits would also document strong and positive biotic effects, whereas those along low-latitude/altitude limits would detect strong and positive associations with abiotic factors. Accordingly, we tallied the number of positive and negative abiotic factors and biotic factors along each edge and provide results in Table 2 of the manuscript, which includes 138 studies that evaluated both abiotic and biotic factors, and those that only include abiotic or biotic factors (n = 78) are listed in Table S4. For distribution-level studies we also tallied the number of studies that documented range shifts along high-latitude/altitude or low-latitude/altitude limits. We summarized the results in Table S5.

To evaluate if there were any potential biases from our non-systematic search, we conducted Fisher-exact tests of independence to 1) determine if the frequency of positive, neutral, or negative abiotic and biotic factors along range edges (High/Low) differed between search types, and 2) the frequency of biotic interactions differed between search types. We set $\alpha = 0.05$ and considered our systematic review to be biased if $P < 0.05$. All analyses were performed using the ‘fisher.test’ function in R (R Development Core Team, 2018). We did not find any statistical differences between search types for the frequency of positive, neutral, and negative 1) abiotic factors along high-latitude/altitude limits ($P = 0.636$), 2) abiotic factors along low-latitude/altitude limits ($P = 0.306$), and 3) biotic factors along low-latitude/altitude limits ($P = 0.332$). Our non-systematic review found a higher frequency of studies that reported positive biotic factors along high-latitude/altitude limits ($P = 0.044$). However, the systematic review also indicated a higher number of positive, rather than negative, biotic factors along upper range limits. Finally, we did not detect any differences between search types for the frequency of biotic interactions along high- and low-latitude/altitude limits ($P = 1$). Overall, we considered the additional entries provided by our non-systematic review to be complementary, with only a slight positive bias towards positive biotic factors along high latitude/altitude limits. Summaries of data used for these tests are listed in Table S6 and Table S7.

We used a similar approach to evaluate the extent to which biotic interactions varied by trophic level. Of the 290 entries, 96 evaluated biotic interactions. We compared the frequency of biotic interaction types (competition and predation/parasitism) between carnivores and herbivores. We found a higher frequency of competitive interactions for carnivores compared to herbivores ($P < 0.0001$); the latter were more influenced by predation and parasitism. To evaluate support for the RLT prediction of negative biotic interactions limiting low-latitude/altitude populations, we compared the frequency of biotic interactions between high-latitude/altitude and low-latitude/altitude limits for carnivores and herbivores. There were no significant differences between trophic levels ($P = 0.456$); negative biotic interactions occurred more frequently for both along lower limits. Tabular summaries of these analyses are provided in Table 1.3 of the manuscript.

Table S1. List of the taxonomic orders, families, and genera included in the systematic review.

Order	Family	Genera
Carnivora	Felidae	Lynx Puma*
	Mustelidae	Pekania Martes Mustela Gulo
	Canidae	Canis Vulpes Urocyon*
	Ursidae	Ursus
	Procyonidae	Procyon**
Didelphimorphia	Didelphidae	Didelphis
Artiodactyla	Cervidae	Alces Odocoileus Cervus Rangifer
	Bovidae	Ovis**
Lagomorpha	Leporidae	Lepus Sylvilagus
	Ochotonidae	Ochotona**
Rodentia	Sciuridae	Sciurus Tamiasciurus* Glaucomys Tamias Marmota* Urocitellus Poliocitellus** Cynomys**
	Erethizontidae	Erethizon
	Cricetidae	Peromyscus Microtus Myodes Lemmus* Synaptomys* Dicrostonyx
	Dipodidae	Napaeozapus**
	Castoridae	Castor**

*No results returned for these genera.
**New genera included in review from systematic search.

Table S2. Total number of results (T) and relevant papers (R) from systematic searches performed from 23–31 January 2019 using Google Scholar (GS) and Web of Science (WOS).

Search Engine*	Search	Search Date	Search String	T	R
WOS	First	1/25/2019	TS=("Range Limit*" OR "Range Edge*") AND TS=(Lynx OR Puma OR Pekania OR Martes OR Gulo OR Canis OR Vulpes OR Didelphis OR Alces OR Odocoileus OR Cervus OR Rangifer OR Lepus OR Sylvilagus OR Sciurus OR Tamiasciurus OR Glaucomys OR Urocitellus OR Erethizon OR Peromyscus OR Microtus OR Myodes OR Lemmus OR Mustela OR Urocyon OR Ursus OR Tamias OR Marmota OR Synaptomys OR Dicrostonyx)	63	33
GS	First	1/23/19 - 1/24/19	"Range Limit" OR "Range Edge" OR "Range Limits" OR "Range Edges" Lynx OR Puma OR Pekania OR Martes OR Gulo OR Canis OR Vulpes OR Didelphis OR Alces OR Odocoileus OR Cervus OR Rangifer OR Lepus OR Sylvilagus OR Sciurus OR Tamiasciurus OR Glaucomys OR Urocitellus OR Erethizon OR Peromyscus OR Microtus OR Myodes OR Lemmus OR Mustela OR Urocyon OR Ursus OR Tamias OR Marmota OR Synaptomys OR Dicrostonyx	6,620	131
WOS	Second	1/25/2019	TS=(Abiotic AND Biotic AND Distribution) AND TS=("Range Limit*" OR "Range Edge*") AND TS=(Lynx OR Puma OR Pekania OR Martes OR Gulo OR Canis OR Vulpes OR Didelphis OR Alces OR Odocoileus OR Cervus OR Rangifer OR Lepus OR Sylvilagus OR Sciurus OR Tamiasciurus OR Glaucomys OR Urocitellus OR Erethizon OR Peromyscus OR Microtus OR Myodes OR Lemmus OR Mustela OR Urocyon OR Ursus OR Tamias OR Marmota OR Synaptomys OR Dicrostonyx)	11	2
GS	Second	1/24/2019	Abiotic Biotic Distribution "Range Limit" OR "Range Edge" OR "Range Limits" OR "Range Edges" Lynx OR Puma OR Pekania OR Martes OR Gulo OR Canis OR Vulpes OR Didelphis OR Alces OR Odocoileus OR Cervus OR Rangifer OR Lepus OR Sylvilagus OR Sciurus OR Tamiasciurus OR Glaucomys OR Urocitellus OR Erethizon OR Peromyscus OR Microtus OR Myodes OR Lemmus OR Mustela OR Urocyon OR Ursus OR Tamias OR Marmota OR Synaptomys OR Dicrostonyx	1758	40

*GS has a 256-character limit, so we performed 3 searches for each search criteria splitting the names of genera to accommodate this limit and to ensure consistency with searches performed on WOS.

Table S2. Total number of results (T) and relevant papers (R) from systematic searches performed from 23–31 January 2019 using Google Scholar (GS) and Web of Science (WOS).

Search Engine*	Search	Search Date	Search String	T	R
WOS	Third	1/31/2019	TS=(Distribution*) AND TS=(Abiotic OR Biotic) AND TS=(Lynx OR Bobcat OR Puma OR Cougar OR “Mountain lion*” OR Pekania OR Fisher OR Martes OR Marten* OR Gulo OR Wolverine* OR Canis OR Coyote* OR Wolf* OR Vulpes OR Fox* OR Didelphis OR Opossum* OR Alces OR Moose OR Odocoileus OR Deer OR Cervus OR Elk OR Rangifer OR Caribou OR Reindeer OR Lepus OR Hare* Or Sylvilagus OR Rabbit* OR Sciurus OR Squirrel* OR Tamiasciurus OR Glaucomys OR “Flying squirrel*” OR Urocitellus “Ground squirrel*” OR Erethizon OR Porcupine* OR Peromyscus OR Mouse OR Mice OR Microtus OR Vole* OR Myodes “Red backed vole*” OR Lemmus OR Lemming* OR Mustela OR Weasel* OR Urocyon OR “Gray fox*” OR “Grey fox*” OR Ursus OR Bear* OR Tamias OR chipmunk* OR Marmota OR Marmot* OR Groundhog* OR Synaptomys OR “Bog lemming*” OR Dicrostonyx OR “Collared lemming*”)	358	19
WOS	Fourth	1/31/2019	TS=(Distribution*) AND TS=(Abiotic OR Biotic) AND TS=(“Range Limit*” OR “Range Edge*”) AND TS=(Lynx OR Bobcat OR Puma OR Cougar OR “Mountain lion*” OR Pekania OR Fisher OR Martes OR Marten* OR Gulo OR Wolverine* OR Canis OR Coyote* OR Wolf* OR Vulpes OR Fox* OR Didelphis OR Opossum* OR Alces OR Moose OR Odocoileus OR Deer OR Cervus OR Elk OR Rangifer OR Caribou OR Reindeer OR Lepus OR Hare* Or Sylvilagus OR Rabbit* OR Sciurus OR Squirrel* OR Tamiasciurus OR Glaucomys OR “Flying squirrel*” OR Urocitellus “Ground squirrel*” OR Erethizon OR Porcupine* OR Peromyscus OR Mouse OR Mice OR Microtus OR Vole* OR Myodes “Red backed vole*” OR Lemmus OR Lemming* OR Mustela OR Weasel* OR Urocyon OR “Gray fox*” OR “Grey fox*” OR Ursus OR Bear* OR Tamias OR chipmunk* OR Marmota OR Marmot* OR Groundhog* OR Synaptomys OR “Bog lemming*” OR Dicrostonyx OR “Collared lemming*”)	9	4
WOS	Fifth	1/31/2019	TS=(Distribution*) AND TS=(“Range Limit*” OR “Range Edge*”) AND TS=(Lynx OR Bobcat OR Puma OR Cougar OR “Mountain lion*” OR Pekania OR Fisher OR Martes OR Marten* OR Gulo OR Wolverine* OR Canis OR Coyote* OR Wolf* OR Vulpes OR Fox* OR Didelphis OR Opossum* OR Alces OR Moose OR Odocoileus OR Deer OR Cervus OR Elk OR Rangifer OR Caribou OR Reindeer OR Lepus OR Hare* Or Sylvilagus OR Rabbit* OR Sciurus OR Squirrel* OR Tamiasciurus OR Glaucomys OR “Flying squirrel*” OR Urocitellus “Ground squirrel*” OR Erethizon OR Porcupine* OR Peromyscus OR Mouse OR Mice OR Microtus OR Vole* OR Myodes “Red backed vole*” OR Lemmus OR Lemming* OR Mustela OR Weasel* OR Urocyon OR “Gray fox*” OR “Grey fox*” OR Ursus OR Bear* OR Tamias OR chipmunk* OR Marmota OR Marmot* OR Groundhog* OR Synaptomys OR “Bog lemming*” OR Dicrostonyx OR “Collared lemming*”)	65	22

Table S3. Number of studies that found positive, negative, and neutral effects of abiotic and biotic factors on the distribution or abundance of North American mammalian carnivores and herbivores. **Note**: This table only includes studies that evaluated abiotic *and* biotic factors along range limits (n = 138).

Trophic Level	**Range-limit**	**Factor**	**Positive**	**Negative**	**Neutral**	**Biotic interaction**[a]	**Total** [b]
Carnivore	High	Abiotic	5	37	0		42
		Biotic	36	7	4	0	47
	Low	Abiotic	29	3	5		37
		Biotic	25	7	3	4	39
Herbivore	High	Abiotic	8	24	1		33
		Biotic	21	11	3	3	38
	Low	Abiotic	17	12	6		35
		Biotic	24	5	1	5	35

[a] Few studies coincidentally evaluated biotic interactions (e.g., competition, predation) at broader spatial scales.

[b] Note that some studies documented multiple abiotic or biotic factors, which occasionally had opposite signs. For example, if a study indicated that one abiotic variable had a positive effect, and another had a strong negative effect, we tallied these as separate records, which increased the total number of studies.

Table S4. Number of studies that found positive, negative, and neutral effects of abiotic and biotic factors and biotic interactions on the distribution or abundance of North American mammalian carnivores and herbivores. **Note**: This table only includes studies that evaluated abiotic *or* biotic factors along range limits (n = 78).

Trophic Level	**Range-limit**	**Factor**	**Positive**	**Negative**	**Neutral**	**Biotic interaction**[a]	**Total**[b]
Carnivore	High	Abiotic	0	7	0	0	7
		Biotic	11	2	0	0	13
	Low	Abiotic	2	1	0	0	3
		Biotic	10	3	0	0	13
Herbivore	High	Abiotic	2	4	0	0	6
		Biotic	10	0	0	0	10
	Low	Abiotic	8	1	0	0	9
		Biotic	12	6	0	0	18

[a] Relatively few studies coincidentally evaluated biotic interactions (e.g., competition, predation) at broader spatial scales.

[b] Note that some studies documented multiple abiotic or biotic factors, which occasionally had opposite signs. For example, if a study indicated that one abiotic variable had a positive effect, and another had a strong negative effect, we tallied these as separate records, which increased the total number of studies.

Table S5. Number of studies reporting range contraction, expansion, and stability along high-latitude/altitude and low-latitude/altitude limits.

Range-limit	Contraction	Expansion	Stability
High	4	13	1
Low	14	5	2

Table S6. Number of studies from our systematic and non-systematic review, and those that overlapped, which reported positive, neutral, or negative abiotic and biotic factors along range limits.

Review Type	Factor	Range-limit	Positive	Neutral	Negative
Systematic review	Abiotic	High	3	1	17
		Low	16	7	7
Non-systematic review		High	4	0	30
		Low	19	3	3
Overlap		High	5	0	13
		Low	10	0	5
Systematic review	Biotic	High	13	4	9
		Low	23	1	8
Non-systematic review		High	28	3	4
		Low	17	3	3
Overlap		High	16	0	5
		Low	8	0	1

Table S7. Number of studies from our systematic and non-systematic review, and those that overlapped, which reported biotic interactions along range limits.

Range-limit	Systematic review	Overlap	Non-systematic review
Low	21	13	28
High	12	2	16

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APPENDIX B

SUPPLEMENTAL: ABIOTIC STRESS AND BIOTIC FACTORS MEDIATE RANGE DYNAMICS ON OPPOSING EDGES: A TEST OF INTERACTIVE RANGE-LIMIT THEORY (IRLT)

Text A1. Overview of Structural Equation Modeling (SEM) or Causal Modeling

Structural equation modeling (SEM), or causal modeling, is a quantitative framework that is increasingly used for evaluating multivariate relationships in ecology (Grace, 2008). However, SEM has been used by economists and social scientists since the 1950s (Pearl, 2012; Shipley, 2016). Sewell Wright, the famous geneticist, is credited with the conceptual development of development SEM but not the analytical development (Shipley, 2016). Wright's paper "Correlation and Causation" was hotly debated by Ronald A. Fisher and Karl Pearson, who are largely credited with the development of randomized and controlled experiments, respectively (Shipley, 2016). SEM continues to be controversial due its claim of causality and how this applies to observational studies that are not able to be physically controlled like experimental studies (Pearl, 2012). However, statistical controls can be viewed as similar to physical or experimental controls in that they allow one to predict how associations among variables change when others are held at their constant (Shipley, 2016).

So what is SEM and how does it differ from correlative statistics? SEM is generally described as a series of univariate regressions within a causal graph or network of paths that provides for the evaluation of complex and competing hypotheses (Grace & Bollen, 2008). Correlative approaches are well-suited for studying single processes or responses and, of course, only measure associations. SEM, on the other hand, allows one to study the direct and indirect effects that influence processes within systems. The primary mathematical difference between SEM and correlational models is the equivalence function, i.e., X→Y is not the same as X=Y. SEM allows one to evaluate 1) interactions between processes, 2) how the effects of a variable (or variables) moves through a system, and 3) how features of a particular system will act in nature given other controlling factors (Shipley, 2016). As such, it is increasingly used to evaluate various ecological theories (Deguines, Brashares, & Prugh, 2017; Peoples, Blanc, & Frimpong, 2015; Prugh & Sivy, 2020; Sivy, Pozzanghera, Grace, & Prugh, 2017; Stoessel, Elmhagen, Vinka, Hellström, & Angerbjörn, 2019).

SEMs generally fit into two different categories. First, the global estimation approach (hereafter global SEM) evaluates a single variance-covariance matrix in which the hypothesized causal system is evaluated on the entire dataset, i.e., all the variables in the system (Shipley, 2016). The second approach, developed by Shipley (2000), uses what is referred to as a local approach (also known as piecewise SEM) that evaluates each response separately to evaluate causal relationships (Lefcheck, 2016; Shipley, 2016). This type of SEM is also referred to as a path model and incorporates elements from graph theory (Shipley, 2016). These two approaches to SEM come with various advantages, assumptions, and limitations (Grace, 2008; Lefcheck, 2016; Shipley, 2009, 2016). I will elaborate on these in the following paragraphs.

As discussed previously, global SEMs evaluate a single variance-covariance matrix to evaluate how well the model fits the data. Model fit is typically determined using a chi-square test to determine how well the modeled variance-covariance matrix fits the data (i.e., the observed variance-covariance matrix). For example, if a global SEM has a chi-squared statistic χ^2 that is not different than 0 (i.e., a failure to reject a null hypothesis), it means that the modeled and observed variance-covariance matrices are similar and considered to be a good model ($P > 0.05$). If a SEM passes this test it can be used for inference and prediction. Global SEMs can incorporate latent and composite variables (e.g., body condition) as well as observed variables. However, a major drawback of the global SEM is that it that assumes errors are normally distributed. Thus, global SEMs are of limited use for ecological studies that include data with non-normal distributions (e.g., count and detection/non-detection data). Further, global models require larger sample sizes which may cause problems for complex SEMs with many variables. Fortunately, local, or piecewise SEMs relax some of these assumptions and allow for non-normal distributions.

Local or piecewise SEMs evaluate each causal relationship individually which allows greater flexibility such as the ability to evaluate a variety of distributions, including those with normal and non-normal data (Shipley, 2016). It also relaxes sample size requirements as each regression is evaluated individually (Grace & Bollen, 2008) and allows for the inclusion of hierarchical models with nested structures and random effects (Lefcheck, 2016). However, because models are evaluated individually, the same assumptions that apply to traditional correlative approaches (e.g., independent errors and homogeneity of variance) also apply to piecewise SEM (Grace, 2008). Therefore, one needs to evaluate individual models using standard diagnostic tests (e.g., residual plots) prior to including in the piecewise SEM to ensure each does not violate assumptions. A drawback of using piecewise SEM is that it only accommodates observed variables but not latent or composite ones (Shipley, 2009). To evaluate the goodness of fit of a piecewise model, there are one or more tests of conditional independence or separation within a casual model; these are referred to as d-sep tests, or tests of directed separation that evaluate whether or not there is a causal structure within the system (Shipley, 2016). Tests of directed separation explicitly evaluate if two or more variables within a causal system, separated by one or more nodes, are statistically independent (i.e., unrelated), accounting for all other relationships (i.e., variables) within the system (Shipley, 2009). Tests of conditional separation use a Fisher's C statistic, which fits a χ^2 distribution with 2 times the number of degrees of freedom, and evaluated using a χ^2 test, with $P > 0.05$ indicating conditional separation (Shipley, 2009). This approach to evaluating model fit is like the global SEM and, similarly, inference and prediction can be made on models that are shown to be d-sep or conditionally separated.

For Chapters 2 and 4 of my dissertation, I used piecewise SEMs or path models to disentangle the effects of climate and biotic factors on species' range limits. As a guide, I will provide a toy example and the necessary terminology for interpreting a piecewise SEM, although, most of it is also applicable to a global SEM. Path models are constructed using a directed acyclic graph (DAG) that is borrowed from graph theory (Shipley, 2016). Consider this simple DAG: $X \rightarrow Z \rightarrow Y$ (remember → indicates causation, whereas = assumes an equivalency). The primary properties of this DAG are as follows: first, it is transitive (if X causes Z, then X also causes Y); second, it is Markovian, meaning that effects are only caused by direct or proximate causes (e.g., Z is directly caused by X, yet Y is only caused by X based on the condition of Z); third, the relationships are irreflexive, meaning that variables cannot cause themselves (although feedback loops over time can be incorporated, e.g., density-dependence). Finally, the relationships are asymmetric, i.e., there are clear causes and effects unless feedback loops are present. For causal models, there are variables within a system that are exogenous and endogenous that have causal roles and/or dependencies: exogenous variables are those that only affect other variables, whereas endogenous variables can affect and be affected by other variables. For the DAG (X→Z→Y), X is an exogenous variable, Z is an endogenous variable that is caused by Z and causes Y, and Y is a terminal endogenous variable, meaning that it is only caused by something else, at least within this causal model. There is only one independence statement within this simple path model: Is X statistically independent of Y given all other relationships within the DAG? If it passes the test (i.e., $P > 0.05$), then inference can be made on it. The direct effects are simply the effect of X on Z and the effect of X on Y, i.e., the path coefficients. The indirect effect of this DAG is the product of the two path coefficients. Of note, this example does not include free covariances or correlated errors. These are user-specified relationships between variables that are assumed to be correlated with each other but do not have causal relationships. I specified correlated errors for the DAGs in Chapters 2 and 4 (e.g., snow depth and forest biomass) to account for features of the system that were potentially correlated but not causally related. The properties and terms introduced in this paragraph generally describe the anatomy of a piecewise SEM and should help in the interpretation of Chapters 2 and 4.

As intimated earlier, adopting a SEM modeling approach allows one to evaluate complex hypotheses to develop a mechanistic understanding of ecological communities (Grace, 2008). However, complex models typically require advanced knowledge that may only come from years of experience within a particular system. This is indeed a feature and drawback of casual modeling. For natural resource managers (and ecologists) that have worked decades within a system, this approach to understanding ecological systems is ideal (Grace, 2008). Further, most biologists are well-suited for learning SEM, given their background in subjects such as regression and statistical modeling (Grace, 2008). Ideally, an SEM-based approach could be coupled with decision science (e.g., structured decision making; Robinson et al., 2016) that brings together subject matter experts to solved complex problems. This approach could be used to develop *a priori* hypotheses of systems that could be tested by stakeholders and used to make management and conservation decisions (Grace & Bollen, 2008; Lefcheck, 2016). Chapters 2 and 4 of my dissertation provide examples of how SEM can be used to evaluate ecological theory and inform conservation and management decisions.

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Table A1. The number of parameters (K), Akaike Information Criterion Score (AIC), delta AIC (ΔAIC), and model weights (w_i) for top competing detection probability models of carnivore species from camera trap data collected from 9 January 2014–12 July 2019 in New Hampshire and Vermont, USA. **Note**: Only the top 10 of 48 detection models are shown for brevity. Top models (**bold**) were chosen based on lowest AIC scores and fewest number of parameters.

bobcat (*Lynx rufus*)

Model*	**K**	**AIC**	**ΔAIC**	w_i
Depth_Bio_TSC_Wk2	**23**	**1783.63**	**0**	**0.61**
Depth_Tmp_Bio_TSC_Wk2	24	1785.54	1.91	0.24
Depth_Bio_TSC_Wk	22	1787.12	3.49	0.11
Depth_Tmp_Bio_TSC_Wk	23	1789.12	5.49	0.04
Depth_Bio_Wk2	22	1796.00	12.37	0.00
Depth_TSC_Wk	21	1797.82	14.19	0.00
Depth_Tmp_Bio_Wk2	23	1797.97	14.34	0.00
Depth_Bio_Wk	21	1799.45	15.82	0.00
Depth_TSC_Wk2	22	1799.71	16.08	0.00
Depth_Tmp_TSC_Wk	22	1799.78	16.15	0.00

Canada lynx (*Lynx canadensis*)

Model*	**K**	**AIC**	**ΔAIC**	w_i
Tmp_TSC_Wk2	22	688.75	0	0.09
Tmp_Bio_TSC_Wk2	23	689.10	0.36	0.07
Depth_TSC	**20**	**689.61**	**0.87**	**0.06**
Tmp_Wk2	21	689.76	1.02	0.05
Depth_Bio_TSC	21	689.86	1.11	0.05
Tmp_Bio_Wk2	22	690.33	1.58	0.04
Depth_Tmp_TSC_Wk2	23	690.37	1.62	0.04
Depth_Tmp_Bio_TSC_Wk2	24	690.53	1.79	0.04
Depth_Tmp_TSC	21	690.83	2.08	0.03
Depth	19	690.91	2.16	0.03

fisher (*Pekania pennanti*)

Model*	**K**	**AIC**	**ΔAIC**	w_i
Depth_Tmp_Bio_TSC_Wk2	**24**	**6049.97**	**0**	**0.82**
Tmp_Bio_TSC_Wk2	23	6052.99	3.03	0.18
Depth_Bio_TSC_Wk2	23	6065.37	15.41	0.00
Bio_TSC_Wk2	22	6074.83	24.86	0.00
Depth_Bio_TSC_Wk	22	6094.16	44.19	0.00
Depth_Tmp_Bio_TSC_Wk	23	6094.76	44.79	0.00
Bio_TSC_Wk	21	6096.64	46.67	0.00
Tmp_Bio_TSC_Wk	22	6098.48	48.51	0.00
Tmp_Bio_TSC	21	6119.83	69.86	0.00
Depth_Bio_TSC	21	6120.77	70.81	0.00

American marten (*Martes americana*)

Model*	**K**	**AIC**	**ΔAIC**	w_i
Tmp_Bio_TSC_Wk2	**23**	**3567.18**	**0**	**0.35**
Depth_Tmp_Bio_TSC_Wk2	24	3568.17	1.00	0.21
Tmp_Bio_TSC_Wk	22	3569.30	2.12	0.12
Depth_Tmp_Bio_TSC_Wk	23	3570.33	3.15	0.07
Depth_Bio_TSC_Wk	22	3570.68	3.50	0.06
Bio_TSC_Wk	21	3571.64	4.47	0.04
Tmp_TSC_Wk2	22	3571.98	4.80	0.03
Depth_Tmp_TSC_Wk2	23	3572.58	5.41	0.02
Depth_Bio_TSC_Wk2	23	3572.65	5.47	0.02
Bio_TSC_Wk2	22	3573.50	6.33	0.02

coyote (*Canis latrans*)

Model*	**K**	**AIC**	**ΔAIC**	w_i
Depth_Tmp_TSC_Wk	**22**	**5526.87**	**0**	**0.34**
Depth_Tmp_TSC_Wk2	23	5528.45	1.58	0.16
Depth_TSC_Wk2	22	5528.71	1.84	0.14
Depth_Tmp_Bio_TSC_Wk	23	5528.82	1.95	0.13

red fox (*Vulpes vulpes*)

Model*	**K**	**AIC**	**ΔAIC**	w_i
Depth_Bio_TSC_Wk2	**23**	**2577.64**	**0**	**0.53**
Depth_Tmp_Bio_TSC_Wk2	24	2578.07	0.43	0.42
Tmp_Bio_TSC_Wk2	23	2585.55	7.91	0.01
Depth_Bio_TSC_Wk	22	2585.55	7.91	0.01

Depth_Bio_TSC_Wk	22	5529.30	2.43	0.10
Depth_Tmp_Bio_TSC_Wk2	24	5530.41	3.54	0.06
Depth_Bio_TSC_Wk2	23	5530.67	3.80	0.05
Depth_Wk	20	5534.87	8.00	0.01
Depth_Tmp_Wk	21	5535.75	8.88	0.00
Depth_Bio_Wk	21	5536.73	9.86	0.00

Depth_Tmp_Bio_TSC_Wk	23	2585.72	8.08	0.01
Depth_Bio_Wk2	22	2586.59	8.95	0.01
Depth_Tmp_Bio_Wk2	23	2587.01	9.37	0.00
Depth_Tmp_TSC_Wk2	23	2587.41	9.77	0.00
Bio_TSC_Wk2	22	2588.28	10.64	0.00
Bio_TSC_Wk	21	2591.27	13.63	0.00

*****Depth = Snow depth; Tmp = Temperature; TSC = Weeks since camera check; Bio = Biomass at site; Wk = Julian week; Wk2 = Second-order polynomial of week

Table A2. The number of parameters (K), Akaike Information Criterion Score (AIC), delta AIC (ΔAIC), and model weights (w_i) for top competing detection probability models of prey species from camera trap data collected from 9 January 2014–12 July 2019 in New Hampshire and Vermont, USA. **Note**: Only the top 10 of 48 detection models are shown for brevity. Top models (**bold**) were chosen based on lowest AIC scores and fewest number of parameters.

white-tailed deer (*Odocoileus virginianus*)

Model	K	AIC	ΔAIC	w_i
Depth_Tmp_Bio_Wk	22	5177.08	0	0.29
Depth_Tmp_Bio_Wk2	23	5178.19	1.12	0.16
Depth_Tmp_Bio	**21**	**5178.25**	**1.17**	**0.16**
Depth_Tmp_Bio_TSC_Wk	23	5178.38	1.30	0.15
Depth_Tmp_Bio_TSC_Wk2	24	5179.35	2.27	0.09
Depth_Tmp_Bio_TSC	22	5179.39	2.31	0.09
Depth_Bio_Wk2	22	5181.33	4.26	0.03
Depth_Bio_TSC_Wk2	23	5182.58	5.50	0.02
Depth_Bio	20	5196.69	19.61	0.00
Depth_Bio_TSC	21	5198.66	21.58	0.00

moose (*Alces alces*)

Model	K	AIC	ΔAIC	w_i
Depth_Tmp_Bio_TSC_Wk2	**24**	**7540.09**	**0**	**0.92**
Depth_Tmp_Bio_Wk2	23	7544.92	4.83	0.08
Depth_Tmp_TSC_Wk2	23	7551.91	11.81	0.00
Depth_Tmp_Wk2	22	7556.81	16.72	0.00
Depth_Bio_TSC_Wk2	23	7558.70	18.60	0.00
Depth_Bio_TSC_Wk	22	7561.49	21.40	0.00
Depth_Tmp_Bio_TSC_Wk	23	7562.04	21.95	0.00
Depth_Bio_Wk2	22	7564.50	24.40	0.00
Depth_Tmp_Bio_Wk	22	7565.15	25.06	0.00
Depth_Bio_Wk	21	7565.58	25.49	0.00

porcupine (*Erethizon dorsatum*)

Model	K	AIC	ΔAIC	w_i
Depth_Tmp_Bio_TSC	**18**	**591.56**	**0**	**0.53**
Depth_Tmp_Bio_TSC_Wk	19	593.32	1.76	0.22
Depth_Tmp_Bio_TSC_Wk2	20	595.22	3.66	0.09
Depth_Tmp_Bio	17	595.32	3.76	0.08
Depth_Tmp_Bio_Wk	18	597.25	5.69	0.03
Depth_Bio_TSC_Wk2	19	598.56	7.00	0.02
Depth_Tmp_Bio_Wk2	19	599.23	7.67	0.01
Tmp_Bio_TSC_Wk	18	599.30	7.74	0.01
Tmp_Bio_TSC_Wk2	19	601.29	9.73	0.00
Depth_Bio_Wk2	18	603.11	11.55	0.00

snowshoe hare (*Lepus americanus*)

Model	K	AIC	ΔAIC	w_i
Depth_Bio_TSC_Wk2	**23**	**11302.68**	**0**	**0.66**
Depth_Tmp_Bio_TSC_Wk2	24	11304.04	1.35	0.34
Depth_Tmp_Bio_TSC_Wk	23	11316.13	13.44	0.00
Depth_Bio_TSC_Wk	22	11322.62	19.94	0.00
Depth_Bio_Wk2	22	11343.62	40.93	0.00
Depth_Tmp_Bio_Wk2	23	11345.25	42.56	0.00
Depth_Tmp_Bio_Wk	22	11361.78	59.10	0.00
Depth_Bio_Wk	21	11374.98	72.30	0.00
Tmp_Bio_TSC_Wk2	23	11392.50	89.82	0.00
Bio_TSC_Wk2	22	11399.28	96.59	0.00

*****Depth = Snow depth; Tmp = Temperature; TSC = Weeks since camera check; Bio = Biomass at site; Wk = Julian week; Wk2 = Second-order polynomial of week

Table A2 (continued). The number of parameters (K), Akaike Information Criterion Score (AIC), delta AIC (ΔAIC), and model weights (w_i) for top competing detection probability models of prey species from camera trap data collected from 9 January 2014–12 July 2019 in New Hampshire and Vermont, USA. **Note**: Only the top 10 of 48 detection models are shown for brevity. Top models (**bold**) were chosen based on lowest AIC scores and fewest number of parameters.

gray squirrel (*Sciurus carolinensis*)

Model	K	AIC	ΔAIC	w_i
Depth_Bio_TSC_Wk2	12	970.32	0	0.18
Depth_TSC_Wk2	11	970.59	0.28	0.16
Depth_Bio_Wk2	11	971.39	1.07	0.11
Depth_Wk2	**10**	**971.40**	**1.08**	**0.11**
Depth_Tmp_Bio_TSC_Wk2	13	971.80	1.48	0.09
Depth_Tmp_Bio_TSC_Wk	12	972.23	1.91	0.07
Depth_Tmp_TSC_Wk2	12	972.35	2.03	0.07
Depth_Tmp_Bio_Wk	11	972.85	2.54	0.05
Depth_Tmp_Bio_Wk2	12	972.99	2.68	0.05
Depth_Tmp_Wk2	11	973.21	2.89	0.04

red squirrel (*Tamiasciurus hudsonicus*)

Model	K	AIC	ΔAIC	w_i
Depth_Tmp_Bio_TSC_Wk2	24	5934.89	0	0.47
Depth_Tmp_TSC_Wk2	**23**	**5936.76**	**1.86**	**0.19**
Depth_Tmp_Bio_Wk2	23	5937.30	2.41	0.14
Tmp_Bio_TSC_Wk2	23	5938.26	3.37	0.09
Depth_Tmp_Wk2	22	5939.31	4.42	0.05
Tmp_TSC_Wk2	22	5940.16	5.27	0.03
Tmp_Bio_Wk2	22	5941.19	6.30	0.02
Tmp_Wk2	21	5943.20	8.31	0.01
Depth_Tmp_Bio_TSC_Wk	23	5991.67	56.78	0.00
Depth_Tmp_TSC_Wk	22	5993.26	58.37	0.00

wild turkey (*Meleagris gallopavo*)

Model	K	AIC	ΔAIC	w_i
Depth_Wk2	16	463.15	0	0.22
Wk2	**15**	**464.46**	**1.30**	**0.11**
Depth_Bio_Wk2	17	464.88	1.73	0.09
Depth_TSC_Wk2	17	465.00	1.85	0.09
Depth_Tmp_Wk2	17	465.15	2.00	0.08
Bio_Wk2	16	466.24	3.09	0.05
TSC_Wk2	16	466.30	3.15	0.05
Tmp_Wk2	16	466.33	3.18	0.04
Depth_Bio_TSC_Wk2	18	466.76	3.61	0.04
Depth_Tmp_Bio_Wk2	18	466.88	3.73	0.03

ruffed grouse (*Bonasa umbellus*)

Model	K	AIC	ΔAIC	w_i
Tmp_TSC_Wk	**16**	**1262.97**	**0**	**0.25**
Tmp_Bio_TSC_Wk	17	1263.67	0.70	0.18
Depth_Tmp_TSC_Wk	17	1264.67	1.70	0.11
Tmp_TSC_Wk2	17	1264.95	1.98	0.09
Depth_Tmp_Bio_TSC_Wk	18	1265.04	2.07	0.09
Tmp_Bio_TSC_Wk2	18	1265.65	2.68	0.07
Depth_Tmp_TSC_Wk2	18	1266.63	3.67	0.04
Tmp_Wk	15	1266.67	3.71	0.04
Depth_Tmp_Bio_TSC_Wk2	19	1267.00	4.03	0.03
Tmp_Bio_Wk	16	1267.35	4.38	0.03

*****Depth = Snow depth; Tmp = Temperature; TSC = Weeks since camera check; Bio = Biomass at site; Wk = Julian week; Wk2 = Second-order polynomial of week

Table A3. Goodness-of-fit (GOF) tests to determine how well the top detection probability (ρ) model fit the data. The GOF for each species was evaluated by comparing the sum of squared residuals (SSE) of the top model with the bootstrapped SSEs (500 iterations). The t_0 is the t-value for the SSE of the top model, t_b is the mean of the bootstrapped samples, and the GOF test ($Pr(t_b > t_0)$) is evaluated using a chi-square test based on differences between the expected and the bootstrapped t-statistics. GOF tests were evaluated using the 'parboot' function in the 'unmarked' package. Values close to 0 or 1 indicate lack of fit.

Species	t_0	$t_0 - t_b$	SD	$Pr(t_b > t_0)$
Canada lynx (*Lynx canadensis*)	69	3.5	12.6	0.391
American marten (*Martes americana*)	465	13.9	30.2	0.323
Red fox (*Vulpes vulpes*)	274	6.8	19.2	0.359
Bobcat (*Lynx rufus*)	183	6.1	15.9	0.335
Coyote (*Canis latrans*)	694	9.7	31.0	0.363
Fisher (*Pekania pennanti*)	813	10.3	32.3	0.381
snowshoe hare (*Lepus americanus*)	**1916**	**118.0**	**47.8**	**0.006**
red squirrel (*Tamiasciurus hudsonicus*)	925	7.8	42.6	0.423
ruffed grouse (*Bonasa umbellus*)	111	-0.7	11.4	0.493
moose (*Alces alces*)	1138	40.6	39.6	0.156
white-tailed deer (*Odocoileus virginianus*)	718	26.6	28.7	0.178
wild turkey (*Meleagris gallopavo*)	36	-1.2	7.4	0.533
gray squirrel (*Sciurus carolinensis*)	113	8.2	17.3	0.307
porcupine (*Erithizon dorsatum*)	73	4.1	13.3	0.361

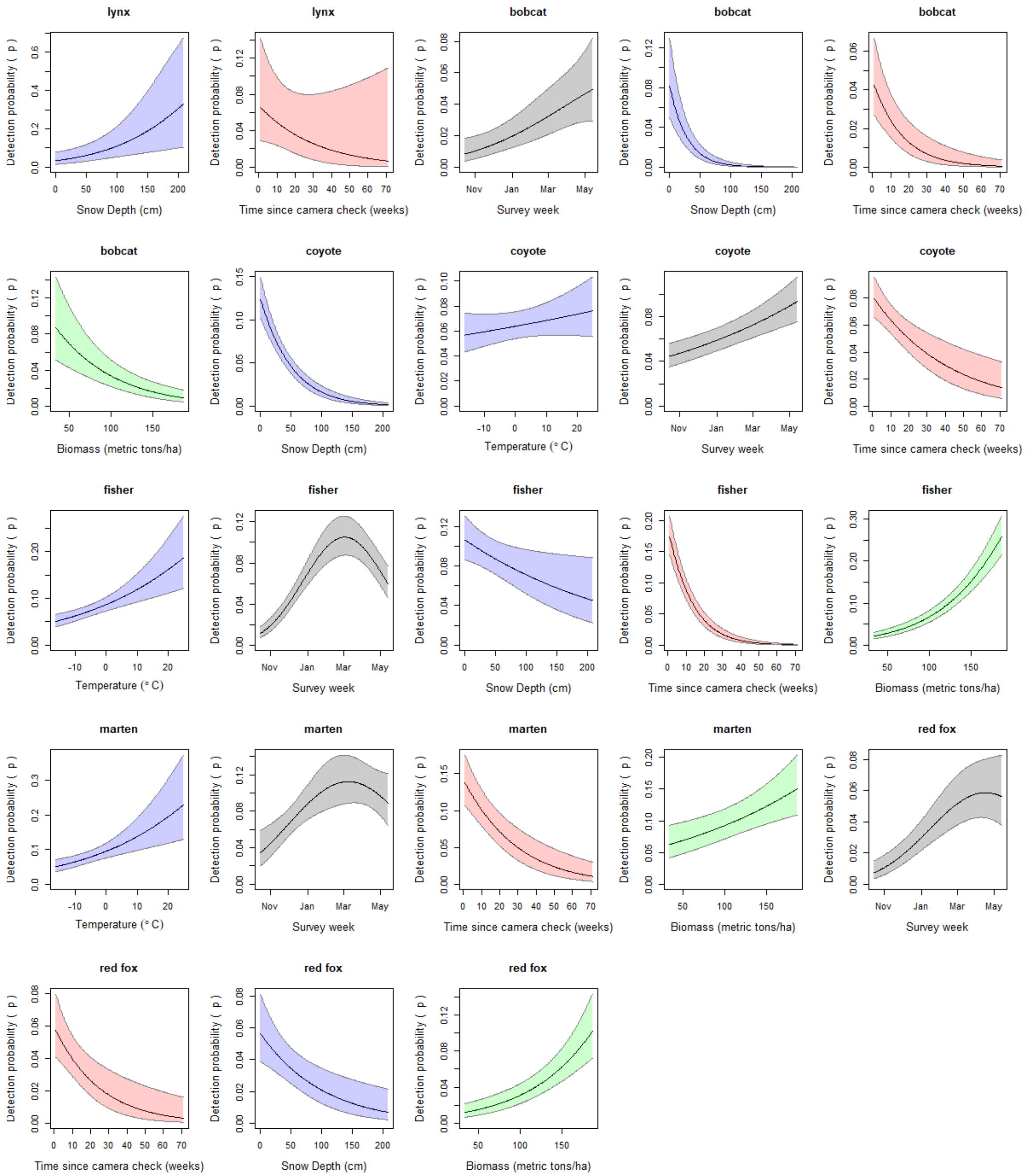

Figure A1. Covariates (Survey week, Temperature, Snow depth, Time since camera check, and Biomass) from top performing detection probability (ρ) models for each carnivore species from camera surveys conducted from 9 January 2014–12 July 2019 in the U.S. states of New Hampshire and Vermont.

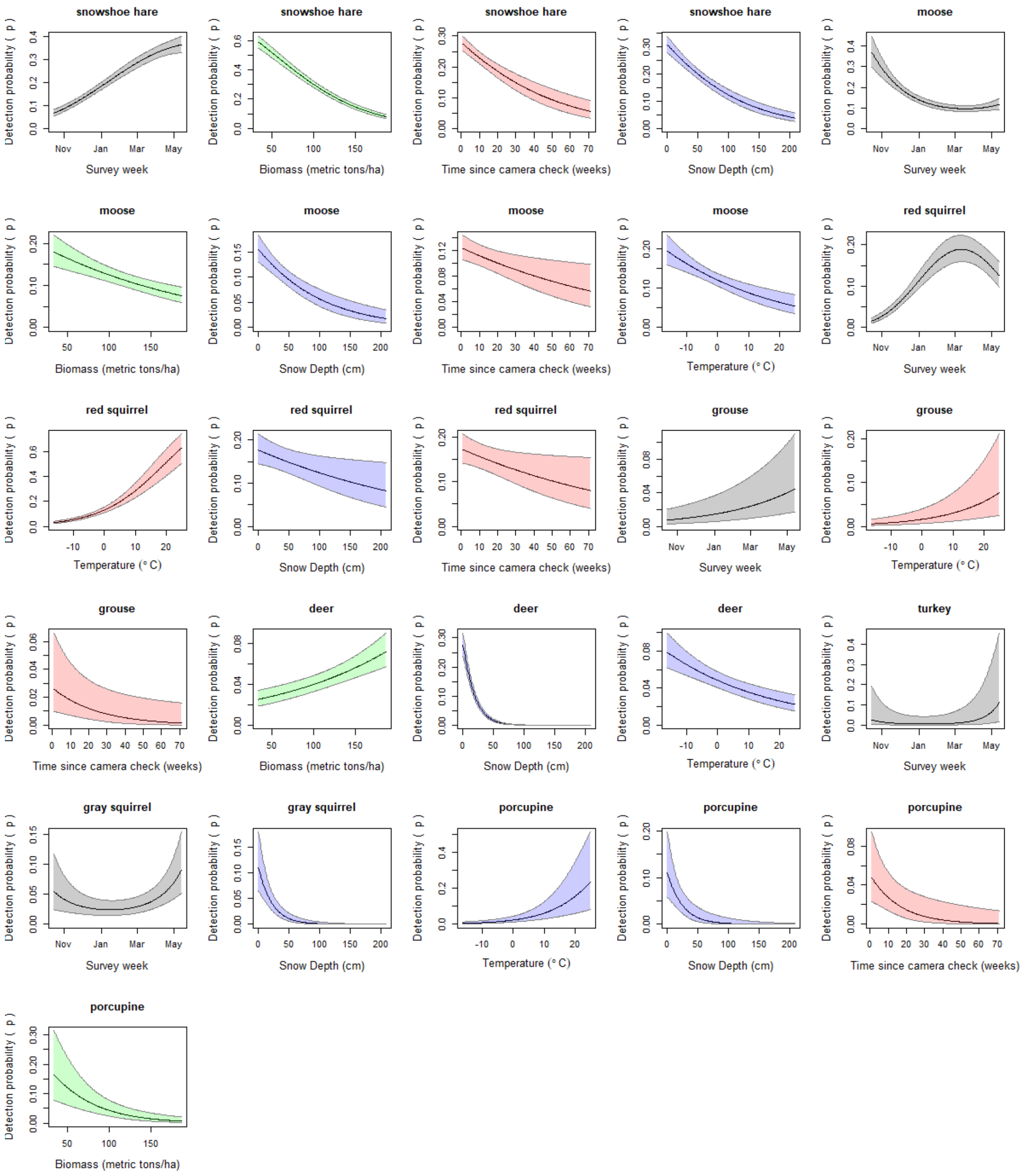

Figure A2. Covariates (Survey week, Temperature, Snow depth, Time since camera check, and Biomass) from top performing detection probability (ρ) models for each prey species from camera surveys conducted from 9 January 2014–12 July 2019 in the U.S. states of New Hampshire and Vermont.

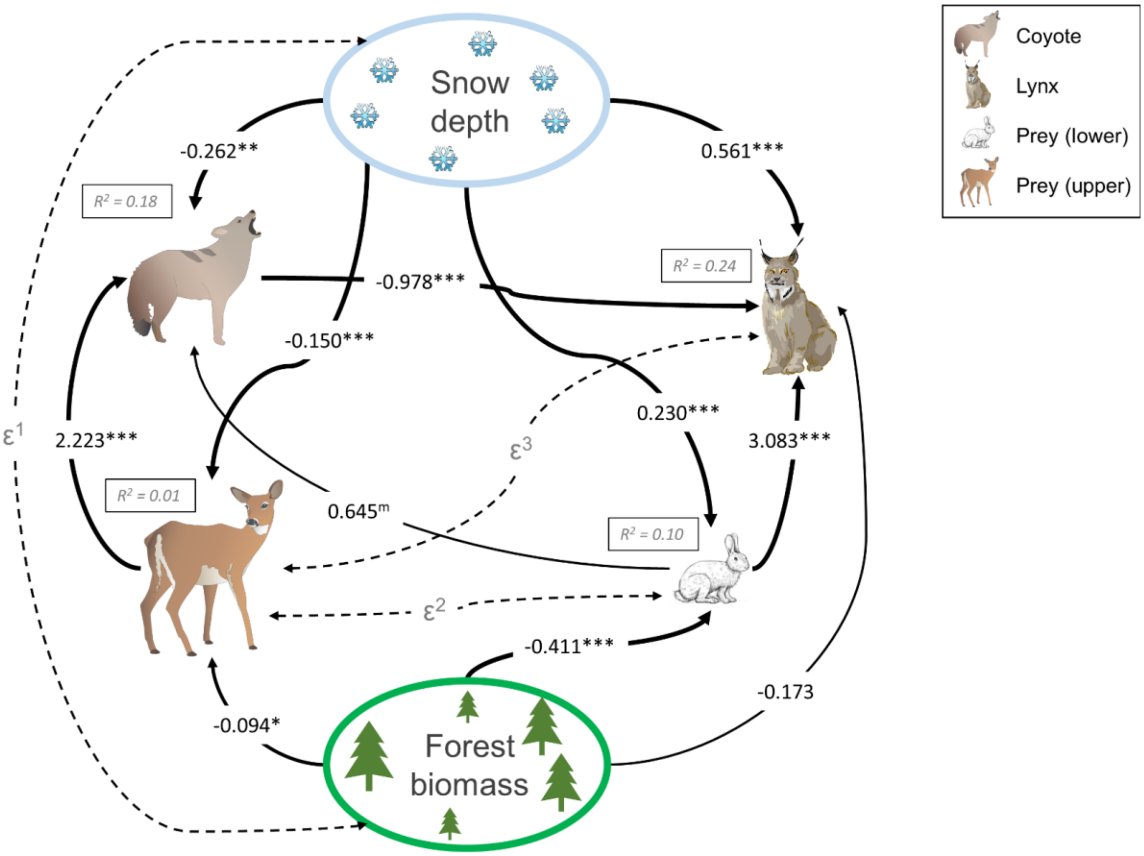

Figure A3. SEM for Canada lynx (*Lynx canadensis*) and coyote (*Canis latrans*) relative to direct and indirect effects of snow depth, prey availability, and forest biomass (metric tons/ha). Solid and unidirectional arrows represent direct effects and dashed bidirectional arrows signify correlated errors among variables. Thick lines indicate significant path coefficients, superscript symbols indicate significance level ($^{\mathrm{m}}P < 0.1$, $*P < 0.05$, $** P < 0.01$, $*** P < 0.001$), and conditional R^2 values are listed within respective nodes. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols).

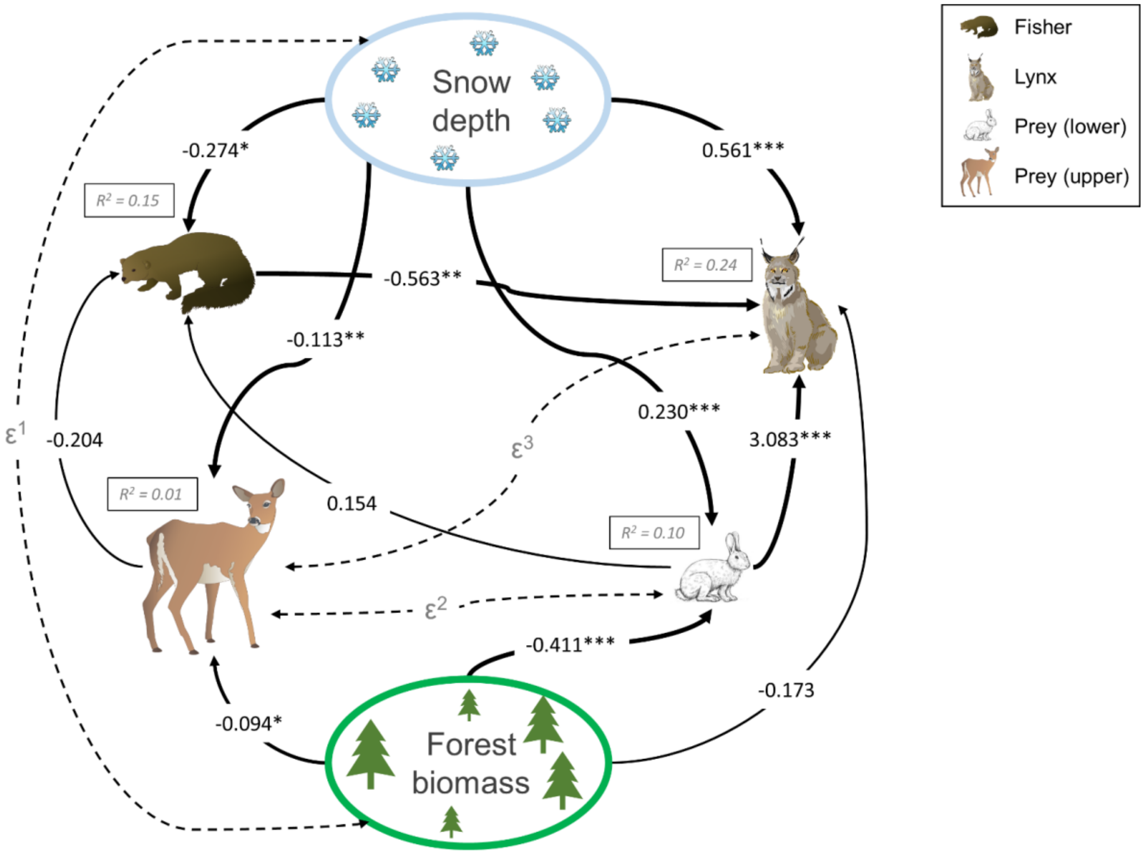

Figure A4. SEM for Canada lynx (*Lynx canadensis*) and fisher (*Pekania pennanti*) relative to direct and indirect effects of snow depth, prey availability, and forest biomass (metric tons/ha). Solid and unidirectional arrows represent direct effects and dashed bidirectional arrows signify correlated errors among variables. Thick lines indicate significant path coefficients, superscript symbols indicate significance level (^{m}P <0.1, **P* <0.05, ** *P* <0.01, *** *P* <0.001), and conditional R^2 values are listed within respective nodes. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols).

APPENDIX C

SUPPLEMENTAL: A GREAT ESCAPE: THE ROLE OF CLIMATE, RESOURCE AVAILABILITY, AND DENSITY-DEPENDENT DYNAMICS ON AN ICONIC HERBIVORE ALONG ITS TRAILING EDGE

Text A1. *Evaluating pellet vs. hare density index*

Methods—To assess the correlation of the pellet-hare density index, we compared stand-level plot density estimates ($\bar{x}$ pellet/ha/month) with stand-level density estimates from live-trap data. We made comparisons from a subset of stands (n = 11 of 60) that spanned the gradient of pellet densities (leaf-off only) sampled in both study areas. To prepare data for evaluating the pellet-hare density index, we followed the approach developed in Maine (Homyack et al., 2006). First, we accounted for differences in pellet accumulation rates, as plots were surveyed at various times during each survey period. We divided the pellet count for individual plots by the number of days that had elapsed since it was previously counted, and then divided this number by the size of the plot (56 cm radius plot = 0.0001 ha) to obtain the pellets/ha/day (Homyack et al., 2006). We then multiplied the pellets/ha/day by the average number of days in a month (30.25) to obtain the pellets/ha/month and calculated the mean pellets/ha/month for each stand (J. A. Homyack et al., 2006).

To produce point estimates for each stand to evaluate the pellet-hare density index, we used spatial capture-recapture (SCR) models (Royle, Fuller, & Sutherland, 2017). First, we evaluated factors influencing encounter probability (p_0) and space use (σ) using an AIC-based approach and chose the best combination of variables to evaluate density (d). During each step, we held the other parameters at their null value (e.g., hold σ

and *d* at “1” while allowing p_0 to vary). For p_0, we considered a trap-specific behavioral response, “session”, and “sex”, and evaluated abiotic (temperature, precipitation) and temporal (Julian day, Julian day^2) variables. We evaluated σ using only “session” and “sex”. Once we determined the best models for p_0 and σ, we evaluated *d* using “session” to obtain density estimates for each stand ($n = 11$). All SCR analyses were performed using the oSCR package in R (Sutherland, Royle, & Linden, 2019). Finally, we performed a linear regression with pellet plot density estimates as the predictor and mark-recapture density estimates as the response variable, as done previously (Berg & Gese, 2010; Homyack et al., 2006; Mills et al., 2005; Murray et al., 2002).

Results—The top SCR model for estimating stand-scale density indicated sex-specific differences in encounter probability, a site-specific behavior response, and no covariates fit on sigma. We used this model to obtain estimates of density (hares/ha) to compare with corresponding estimates of pellet density (mean pellets/ha/month) within the same stands (Table A3). The pellet vs. hare density relationship was significant ($P = 0.003$, $R^2 = 0.64$; Fig. A6), indicating that pellet data was a moderately robust index for evaluating stand-scale density and population fluctuations among the CL, NB, and WMNF regions.

Text A2. *Protocol for conducting mortality investigations*

We listened for each animal weekly to determine its status (active = 35 ppm; mortality = 70 ppm). If an animal was on mortality mode, we first triangulated the animal using our telemetry protocol and then homed in on the animal. When we were close to the animal (~20 m; determined by strength of radio signal) we circled the site, inspecting the area for clues (e.g., disturbed vegetation, predator scats). Once the animal and/or collar was discovered, we recorded 1) a GPS waypoint, 2) a qualitative assessment of forest composition/structure, 3) the weather within the past several days, and 4) any clues that would indicate the cause of mortality. We used a combination of site clues and sign on the radio collar and/or animal (if found) to determine the cause-specific mortality. If the animal was available, we performed a field necropsy, paying close attention to hemorrhaging, punctures, broken bones, etc. The presence and absence of hemorrhaging is indicative of premortem and postmortem wounds, respectively, and can be used to determine if the animal was preyed or scavenged upon (McLellan et al., 2018). Punctures or lacerations on the soft tissue or skin can be used to identify the predator/scavenger. Further, because the protective tubing on collars was a soft plastic, it was susceptible to damage by canines. If canine punctures were present on the animal or collar, we took pictures and recorded distances between canines and matched it with available information (field guide, museum specimens) to determine the predator species (McLellan et al., 2018). We also paid close attention to other clues such as broken bones, location of carcass (e.g., in a tree or subterranean), and the feeding style (cached stomach, clipped feet, piles of fur) to differentiate between mammalian and avian predators.

Text A3. *Estimating landscape-scale density using SCR models*

Methods— We also estimated landscape scale-density using spatial capture-recapture (SCR) models (Royle et al. 2017) to evaluate differences between the NB and WMNF study areas. First, we evaluated factors influencing encounter probability ($\rho0$) and space use (σ) using an AIC-based approach and chose the best combination of variables to evaluate density (*d*). During each step, we held the other parameters at their null value (e.g., hold σ and d at “1” while allowing p0 to vary). For $\rho0$, we considered a trap-specific behavioral response, “session”, and “sex”, and evaluated abiotic (temperature, precipitation) and temporal (Julian day, Julian day^2) variables. We evaluated σ using only “session” and “sex”. Once we determined the best models for $\rho0$ and σ, we evaluated *d* using “session” to obtain density estimates for each landscape (WMNF, NB). All SCR analyses were performed using the oSCR package in R (Sutherland et al. 2019).

Results—The top SCR model for estimating landscape-scale density indicated sex-specific differences in encounter probability, a site-specific behavior response, and session-specific differences in sigma. Encounter probability was significantly lower in the WMNF than the NB and lower for males than females (Table A7). We also found evidence for a strong trap-specific response, indicating hares were more likely to enter traps after their first encounter (Table A7). Hares made significantly longer movements in the WMNF than in the NB (Table A7). Landscape-density estimates were significantly higher in the NB (0.52 hares/ha) than the WMNF (0.10 hares/ha; Table A7, Fig. A5).

Text A4. Institutional Animal Care and Use Committee (IACUC) Notice of Approval for working with snowshoe hares (*Lepus americanus*)

University of Massachusetts Amherst
Research Administration Bldg.
70 Butterfield Terrace
Amherst, MA 01003-9242

Research Compliance
Institutional Animal Care and Use Committee
Telephone: (413) 577-0387
FAX: (413) 577-1728

NOTICE OF APPROVAL

Date: June 09, 2016
Principal Investigator: Morelli Toni, Environmental Conservation
Protocol #: 2016-0024
Protocol Title: Assessing potential impacts of climate change on carnivore occupancy and snowshoe hare demography along elevational and latitudinal gradients in New England
IACUC Approval Period: 06/09/2016 - 05/18/2017 REVISION

The above referenced protocol submitted for review by the Institutional Animal Care and Use Committee has received approval. In compliance with federal regulations and the University of Massachusetts Amherst PHS Assurance, protocol approval is for up to three years contingent upon:

- IACUC approval before making significant changes;
- IACUC approval for the addition of new personnel before they start working with animals;
- Satisfactory update review annually

You will receive a renewal reminder close to the first and second anniversaries of your original approval date. You will need to submit the annual review materials to the IACUC for review via e-protocol at least one week prior to the expiration date to ensure protocol approval is continued. To continue this project past third anniversary of your protocol's original approval date you must submit a new protocol for IACUC review.

If this approval letter was generated following IACUC review of a change to the protocol listed above, this approval applies to the latest version of your protocol.

Jesse Mager, PhD
Chair, Institutional Animal Care and Use Committee

Table A1. The number of parameters (K), Akaike Information Criterion Score (AIC), delta AIC (ΔAIC), and model weights (w_i) for top competing occupancy models of snowshoe hare from camera trap data collected from 9 January 2014–12 July 2019 in New Hampshire and Vermont, USA. **Note**: Only the top 10 of 48 detection models are shown for brevity. The top model (**bold**) was chosen based on lowest AIC scores and fewest number of parameters.

ψ Model	**K**	**AIC**	**ΔAIC**	w_i	r^2
Max depth + Mixedwood + Hardwood	20	11314.350	0.000	0.260	0.126
Depth + Mixedwood + Hardwood	20	11314.380	0.028	0.250	0.126
Snow duration + Biomass^2	20	11314.760	0.408	0.210	0.126
Snow duration + Biomass	**19**	**11315.560**	**1.207**	**0.140**	**0.122**
Snow duration + Mixedwood + Hardwood	20	11315.790	1.438	0.130	0.124
Snow duration + Hardwood^2	20	11321.770	7.424	0.006	0.117
Max depth + Biomass^2	20	11324.730	10.383	0.001	0.114
Depth + Biomass^2	20	11327.100	12.751	0.000	0.111
Snow duration + Hardwood	19	11328.840	14.490	0.000	0.106
Max depth + Biomass	19	11330.920	16.567	0.000	0.104
Snow duration + Boreal^2	20	11332.100	17.749	0.000	0.105

Table A2. Mean (± SE) pellets/ha/month for 6 stand types, 12 sub-stand types, and individual stands (Stand id) established in 2014 (WMNF), 2015 (NB), and 2017 (CL) and resampled during spring and fall to index leaf-off (16 October–15 May) and leaf-on (16 May–15 October) density, respectively.

Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
WMNF	Hardwood (L)	HD	2015	Leaf-on	6HD1	50	39 ± 39
WMNF	Hardwood (L)	HD	2015	Leaf-on	6HD2	50	0 ± 0
WMNF	Hardwood (L)	HD	2015	Leaf-on	6HD3	50	0 ± 0
WMNF	Hardwood (L)	HD	2015	Leaf-on	7HD1	45	0 ± 0
WMNF	Lowland SF (L)	LSF	2015	Leaf-on	6LSF1	50	1104 ± 527
WMNF	Lowland SF (L)	LSF	2015	Leaf-on	6LSF2	50	0 ± 0
WMNF	Lowland SF (L)	LSF	2015	Leaf-on	6LSF3	50	165 ± 99
WMNF	Lowland SF (L)	LSF	2015	Leaf-on	7LSF1	50	43 ± 43
WMNF	Lowland SF (L)	LSF	2015	Leaf-on	8LSF2	45	95 ± 95
WMNF	Mixedwood (L)	MW	2015	Leaf-on	6MW2	50	85 ± 60
WMNF	Mixedwood (L)	MW	2015	Leaf-on	6MW3	50	138 ± 137
WMNF	Mixedwood (L)	MW	2015	Leaf-on	6MW4	50	819 ± 221
WMNF	Mixedwood (L)	MW	2015	Leaf-on	7MW1	45	607 ± 302
WMNF	Mixedwood (L)	MW	2015	Leaf-on	7MW2	45	0 ± 0
WMNF	Mixedwood (L)	MW	2015	Leaf-on	8MW1	45	54 ± 54
WMNF	Mixedwood (L)	MW	2015	Leaf-on	8MW2	45	325 ± 183
WMNF	Montane SF (L)	HSF	2015	Leaf-on	6HSF1	50	216 ± 154
WMNF	Montane SF (L)	HSF	2015	Leaf-on	6HSF3	50	1361 ± 402
WMNF	Montane SF (L)	HSF	2015	Leaf-on	6HSF4	50	244 ± 111
WMNF	Montane SF (L)	KM	2015	Leaf-on	6KM1	50	931 ± 286
WMNF	Montane SF (L)	KM	2015	Leaf-on	6KM2	45	1616 ± 511
WMNF	Montane SF (L)	SFW	2015	Leaf-on	6SFW1	50	1284 ± 534
WMNF	Montane SF (L)	SFW	2015	Leaf-on	6SFW3	50	1047 ± 430
WMNF	Montane SF (L)	SFW	2015	Leaf-on	6SFW5	49	112 ± 112
WMNF	Montane SF (L)	HSF	2015	Leaf-on	7HSF1	50	1182 ± 319
WMNF	Montane SF (L)	HSF	2015	Leaf-on	7HSF2	45	0 ± 0
WMNF	Montane SF (L)	SFW	2015	Leaf-on	7SFW1	50	55 ± 55
WMNF	Montane SF (L)	SFW	2015	Leaf-on	7SFW2	45	691 ± 517
WMNF	Montane SF (L)	HSF	2015	Leaf-on	8HSF2	45	0 ± 0
WMNF	Hardwood (L)	HD	2016	Leaf-on	6HD1	50	261 ± 101
WMNF	Hardwood (L)	HD	2016	Leaf-on	6HD2	50	43 ± 43
WMNF	Hardwood (L)	HD	2016	Leaf-on	6HD3	50	139 ± 78
WMNF	Hardwood (L)	HD	2016	Leaf-on	7HD1	45	316 ± 128
WMNF	Lowland SF (L)	LSF	2016	Leaf-on	6LSF1	50	448 ± 167
WMNF	Lowland SF (L)	LSF	2016	Leaf-on	6LSF2	50	151 ± 112
WMNF	Lowland SF (L)	LSF	2016	Leaf-on	6LSF3	50	229 ± 118
WMNF	Lowland SF (L)	LSF	2016	Leaf-on	7LSF1	50	219 ± 94
WMNF	Lowland SF (L)	LSF	2016	Leaf-on	8LSF2	45	1577 ± 744
WMNF	Lowland SF (L)	LSF	2016	Leaf-on	8LSF3	45	931 ± 263

[a] Montane (≥823 m) and lowland (<823 m) classifications were based on the New Hampshire Wildlife Action Plan classification system (WAP, 2015). E = early seral (25–60 yrs. old). L = late seral (89–295 yrs. old). [b] Sub-stand classification based on (Sperduto & Nichols, 2012). [c] The total number of plots/stand.

Table A2 (continued). Mean (± SE) pellets/ha/month for 6 stand types, 12 sub-stand types, and individual stands (Stand id) established in 2014 (WMNF), 2015 (NB), and 2017 (CL) and resampled during spring and fall to index leaf-off (16 October–15 May) and leaf-on (16 May–15 October) density, respectively.

Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
WMNF	Mixedwood (L)	MW	2016	Leaf-on	6MW2	50	728 ± 263
WMNF	Mixedwood (L)	MW	2016	Leaf-on	6MW3	50	302 ± 137
WMNF	Mixedwood (L)	MW	2016	Leaf-on	6MW4	50	667 ± 252
WMNF	Mixedwood (L)	MW	2016	Leaf-on	7MW1	45	2011 ± 672
WMNF	Mixedwood (L)	MW	2016	Leaf-on	7MW2	45	735 ± 403
WMNF	Mixedwood (L)	MW	2016	Leaf-on	8MW1	45	142 ± 105
WMNF	Mixedwood (L)	MW	2016	Leaf-on	8MW2	45	162 ± 97
WMNF	Montane SF (L)	HSF	2016	Leaf-on	6HSF1	50	550 ± 180
WMNF	Montane SF (L)	HSF	2016	Leaf-on	6HSF3	50	1258 ± 310
WMNF	Montane SF (L)	HSF	2016	Leaf-on	6HSF4	50	313 ± 142
WMNF	Montane SF (L)	KM	2016	Leaf-on	6KM1	50	786 ± 242
WMNF	Montane SF (L)	KM	2016	Leaf-on	6KM2	45	2967 ± 1758
WMNF	Montane SF (L)	SFW	2016	Leaf-on	6SFW1	50	1083 ± 254
WMNF	Montane SF (L)	SFW	2016	Leaf-on	6SFW3	50	4142 ± 1320
WMNF	Montane SF (L)	SFW	2016	Leaf-on	6SFW5	50	978 ± 320
WMNF	Montane SF (L)	HSF	2016	Leaf-on	7HSF1	50	1057 ± 275
WMNF	Montane SF (L)	HSF	2016	Leaf-on	7HSF2	45	0 ± 0
WMNF	Montane SF (L)	SFW	2016	Leaf-on	7SFW1	50	240 ± 116
WMNF	Montane SF (L)	SFW	2016	Leaf-on	7SFW2	45	535 ± 182
WMNF	Montane SF (L)	SFW	2016	Leaf-on	7SFW3	45	460 ± 311
WMNF	Montane SF (L)	HSF	2016	Leaf-on	8HSF1	45	110 ± 77
WMNF	Montane SF (L)	HSF	2016	Leaf-on	8HSF2	45	55 ± 55
WMNF	Lowland SF (L)	LSF	2017	Leaf-on	6LSF1	50	1380 ± 365
WMNF	Lowland SF (L)	LSF	2017	Leaf-on	6LSF3	50	207 ± 124
WMNF	Lowland SF (L)	LSF	2017	Leaf-on	7LSF1	50	136 ± 77
WMNF	Lowland SF (L)	LSF	2017	Leaf-on	8LSF2	45	1980 ± 1018
WMNF	Lowland SF (L)	LSF	2017	Leaf-on	8LSF3	45	594 ± 379
WMNF	Mixedwood (L)	MW	2017	Leaf-on	6MW2	50	517 ± 165
WMNF	Mixedwood (L)	MW	2017	Leaf-on	6MW4	50	526 ± 475
WMNF	Mixedwood (L)	MW	2017	Leaf-on	7MW1	45	1667 ± 473
WMNF	Mixedwood (L)	MW	2017	Leaf-on	8MW2	45	993 ± 431
WMNF	Montane SF (L)	HSF	2017	Leaf-on	6HSF1	50	425 ± 191
WMNF	Montane SF (L)	HSF	2017	Leaf-on	6HSF3	50	1883 ± 873
WMNF	Montane SF (L)	HSF	2017	Leaf-on	6HSF4	50	642 ± 218
WMNF	Montane SF (L)	KM	2017	Leaf-on	6KM1	50	171 ± 127
WMNF	Montane SF (L)	KM	2017	Leaf-on	6KM2	45	2126 ± 547
WMNF	Montane SF (L)	SFW	2017	Leaf-on	6SFW1	50	228 ± 160
WMNF	Montane SF (L)	SFW	2017	Leaf-on	6SFW3	50	1551 ± 443

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[b] Sub-stand classification based on (Sperduto & Nichols, 2012).

[c] The total number of plots/stand.

Table A2 (continued). Mean (± SE) pellets/ha/month for 6 stand types, 12 sub-stand types, and individual stands (Stand id) established in 2014 (WMNF), 2015 (NB), and 2017 (CL) and resampled during spring and fall to index leaf-off (16 October–15 May) and leaf-on (16 May–15 October) density, respectively.

Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
WMNF	Mixedwood (L)	SFW	2017	Leaf-on	6SFW5	50	375 ± 171
WMNF	Mixedwood (L)	HSF	2017	Leaf-on	7HSF1	50	2000 ± 926
WMNF	Mixedwood (L)	SFW	2017	Leaf-on	7SFW1	50	52 ± 52
WMNF	Mixedwood (L)	SFW	2017	Leaf-on	7SFW2	45	328 ± 126
WMNF	Mixedwood (L)	SFW	2017	Leaf-on	7SFW3	45	161 ± 119
WMNF	Mixedwood (L)	HD	2015	Leaf-off	6HD1	50	0 ± 0
WMNF	Mixedwood (L)	HD	2015	Leaf-off	6HD2	50	83 ± 47
WMNF	Montane SF (L)	HD	2015	Leaf-off	6HD3	50	82 ± 61
WMNF	Montane SF (L)	HD	2015	Leaf-off	7HD1	45	0 ± 0
WMNF	Montane SF (L)	LSF	2015	Leaf-off	6LSF1	50	3893 ± 1520
WMNF	Montane SF (L)	LSF	2015	Leaf-off	6LSF2	50	53 ± 53
WMNF	Montane SF (L)	LSF	2015	Leaf-off	6LSF3	50	799 ± 349
WMNF	Montane SF (L)	LSF	2015	Leaf-off	7LSF1	50	2566 ± 1123
WMNF	Montane SF (L)	LSF	2015	Leaf-off	8LSF2	45	702 ± 334
WMNF	Montane SF (L)	MW	2015	Leaf-off	6MW2	50	2393 ± 943
WMNF	Montane SF (L)	MW	2015	Leaf-off	6MW3	50	107 ± 52
WMNF	Montane SF (L)	MW	2015	Leaf-off	6MW4	50	921 ± 269
WMNF	Montane SF (L)	MW	2015	Leaf-off	7MW1	45	1522 ± 414
WMNF	Montane SF (L)	MW	2015	Leaf-off	7MW2	45	390 ± 135
WMNF	Montane SF (L)	MW	2015	Leaf-off	8MW1	45	36 ± 36
WMNF	Montane SF (L)	MW	2015	Leaf-off	8MW2	45	1045 ± 568
WMNF	Montane SF (L)	HSF	2015	Leaf-off	6HSF1	50	610 ± 138
WMNF	Lowland SF (L)	HSF	2015	Leaf-off	6HSF3	50	1726 ± 437
WMNF	Lowland SF (L)	HSF	2015	Leaf-off	6HSF4	50	914 ± 286
WMNF	Lowland SF (L)	KM	2015	Leaf-off	6KM1	50	1051 ± 271
WMNF	Lowland SF (L)	SFW	2015	Leaf-off	6SFW1	50	3238 ± 1162
WMNF	Lowland SF (L)	SFW	2015	Leaf-off	6SFW3	50	2529 ± 602
WMNF	Mixedwood (L)	SFW	2015	Leaf-off	6SFW5	50	614 ± 213
WMNF	Mixedwood (L)	HSF	2015	Leaf-off	7HSF1	50	1994 ± 420
WMNF	Mixedwood (L)	SFW	2015	Leaf-off	7SFW1	50	325 ± 153
WMNF	Mixedwood (L)	SFW	2015	Leaf-off	7SFW2	45	620 ± 156
WMNF	Montane SF (L)	HD	2016	Leaf-off	6HD1	50	54 ± 37
WMNF	Montane SF (L)	HD	2016	Leaf-off	6HD2	50	27 ± 27
WMNF	Montane SF (L)	HD	2016	Leaf-off	6HD3	50	0 ± 0
WMNF	Montane SF (L)	HD	2016	Leaf-off	7HD1	45	0 ± 0
WMNF	Montane SF (L)	LSF	2016	Leaf-off	6LSF1	50	1029 ± 281
WMNF	Montane SF (L)	LSF	2016	Leaf-off	6LSF2	50	0 ± 0
WMNF	Montane SF (L)	LSF	2016	Leaf-off	6LSF3	50	2174 ± 824

[a] Montane (≥823 m) and lowland (<823 m) classifications were based on the New Hampshire Wildlife Action Plan classification system (WAP, 2015). E = early seral (25–60 yrs. old). L = late seral (89–295 yrs. old).

[b] Sub-stand classification based on (Sperduto & Nichols, 2012).

[c] The total number of plots/stand.

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Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
WMNF	Lowland SF (L)	LSF	2016	Leaf-off	7LSF1	50	2709 ± 1199
WMNF	Lowland SF (L)	LSF	2016	Leaf-off	8LSF2	45	2641 ± 1228
WMNF	Lowland SF (L)	LSF	2016	Leaf-off	8LSF3	45	158 ± 103
WMNF	Mixedwood (L)	MW	2016	Leaf-off	6MW2	50	1938 ± 566
WMNF	Mixedwood (L)	MW	2016	Leaf-off	6MW3	50	1240 ± 966
WMNF	Mixedwood (L)	MW	2016	Leaf-off	6MW4	50	966 ± 311
WMNF	Mixedwood (L)	MW	2016	Leaf-off	7MW1	45	4303 ± 1124
WMNF	Mixedwood (L)	MW	2016	Leaf-off	7MW2	45	248 ± 75
WMNF	Mixedwood (L)	MW	2016	Leaf-off	8MW1	45	27 ± 27
WMNF	Mixedwood (L)	MW	2016	Leaf-off	8MW2	45	877 ± 369
WMNF	Montane SF (L)	HSF	2016	Leaf-off	6HSF1	50	1742 ± 973
WMNF	Montane SF (L)	HSF	2016	Leaf-off	6HSF3	50	1986 ± 636
WMNF	Montane SF (L)	HSF	2016	Leaf-off	6HSF4	50	1246 ± 537
WMNF	Montane SF (L)	KM	2016	Leaf-off	6KM1	50	523 ± 230
WMNF	Montane SF (L)	KM	2016	Leaf-off	6KM2	45	310 ± 107
WMNF	Montane SF (L)	SFW	2016	Leaf-off	6SFW1	50	2588 ± 773
WMNF	Montane SF (L)	SFW	2016	Leaf-off	6SFW3	50	1530 ± 668
WMNF	Montane SF (L)	SFW	2016	Leaf-off	6SFW5	50	672 ± 232
WMNF	Montane SF (L)	HSF	2016	Leaf-off	7HSF1	50	1911 ± 354
WMNF	Montane SF (L)	HSF	2016	Leaf-off	7HSF2	45	81 ± 46
WMNF	Montane SF (L)	SFW	2016	Leaf-off	7SFW1	50	1130 ± 269
WMNF	Montane SF (L)	SFW	2016	Leaf-off	7SFW2	45	1450 ± 361
WMNF	Montane SF (L)	SFW	2016	Leaf-off	7SFW3	45	140 ± 92
WMNF	Montane SF (L)	HSF	2016	Leaf-off	8HSF1	45	254 ± 102
WMNF	Montane SF (L)	HSF	2016	Leaf-off	8HSF2	45	156 ± 132
WMNF	Hardwood (L)	HD	2017	Leaf-off	6HD1	50	0 ± 0
WMNF	Hardwood (L)	HD	2017	Leaf-off	6HD2	50	0 ± 0
WMNF	Hardwood (L)	HD	2017	Leaf-off	6HD3	50	26 ± 26
WMNF	Hardwood (L)	HD	2017	Leaf-off	7HD1	44	63 ± 44
WMNF	Lowland SF (L)	LSF	2017	Leaf-off	6LSF1	50	3098 ± 1283
WMNF	Lowland SF (L)	LSF	2017	Leaf-off	6LSF2	50	223 ± 223
WMNF	Lowland SF (L)	LSF	2017	Leaf-off	6LSF3	50	621 ± 445
WMNF	Lowland SF (L)	LSF	2017	Leaf-off	7LSF1	48	871 ± 461
WMNF	Lowland SF (L)	LSF	2017	Leaf-off	8LSF2	45	7876 ± 2846
WMNF	Lowland SF (L)	LSF	2017	Leaf-off	8LSF3	45	527 ± 263
WMNF	Mixedwood (L)	MW	2017	Leaf-off	6MW2	50	1766 ± 582
WMNF	Mixedwood (L)	MW	2017	Leaf-off	6MW3	50	322 ± 226
WMNF	Mixedwood (L)	MW	2017	Leaf-off	6MW4	50	563 ± 216

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Table A2 (continued). Mean (± SE) pellets/ha/month for 6 stand types, 12 sub-stand types, and individual stands (Stand id) established in 2014 (WMNF), 2015 (NB), and 2017 (CL) and resampled during spring and fall to index leaf-off (16 October–15 May) and leaf-on (16 May–15 October) density, respectively.

Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
WMNF	Mixedwood (L)	MW	2017	Leaf-off	7MW1	45	3389 ± 850
WMNF	Mixedwood (L)	MW	2017	Leaf-off	7MW2	45	6398 ± 5389
WMNF	Mixedwood (L)	MW	2017	Leaf-off	8MW1	45	0 ± 0
WMNF	Mixedwood (L)	MW	2017	Leaf-off	8MW2	45	2995 ± 2503
WMNF	Montane SF (L)	HSF	2017	Leaf-off	6HSF1	50	655 ± 133
WMNF	Montane SF (L)	HSF	2017	Leaf-off	6HSF3	50	1126 ± 454
WMNF	Montane SF (L)	HSF	2017	Leaf-off	6HSF4	50	206 ± 77
WMNF	Montane SF (L)	KM	2017	Leaf-off	6KM1	50	235 ± 106
WMNF	Montane SF (L)	KM	2017	Leaf-off	6KM2	45	1537 ± 466
WMNF	Montane SF (L)	SFW	2017	Leaf-off	6SFW1	50	942 ± 456
WMNF	Montane SF (L)	SFW	2017	Leaf-off	6SFW3	50	1580 ± 349
WMNF	Montane SF (L)	SFW	2017	Leaf-off	6SFW5	50	424 ± 266
WMNF	Montane SF (L)	HSF	2017	Leaf-off	7HSF1	50	1623 ± 446
WMNF	Montane SF (L)	HSF	2017	Leaf-off	7HSF2	33	188 ± 122
WMNF	Montane SF (L)	SFW	2017	Leaf-off	7SFW1	48	555 ± 207
WMNF	Montane SF (L)	SFW	2017	Leaf-off	7SFW2	45	784 ± 201
WMNF	Montane SF (L)	SFW	2017	Leaf-off	7SFW3	45	420 ± 165
WMNF	Montane SF (L)	HSF	2017	Leaf-off	8HSF1	45	146 ± 75
WMNF	Montane SF (L)	HSF	2017	Leaf-off	8HSF2	45	0 ± 0
WMNF	Lowland SF (L)	LSF	2018	Leaf-off	6LSF1	50	1415 ± 849
WMNF	Lowland SF (L)	LSF	2018	Leaf-off	6LSF3	50	3241 ± 2944
WMNF	Lowland SF (L)	LSF	2018	Leaf-off	7LSF1	50	733 ± 338
WMNF	Lowland SF (L)	LSF	2018	Leaf-off	8LSF2	45	6598 ± 2068
WMNF	Lowland SF (L)	LSF	2018	Leaf-off	8LSF3	45	620 ± 264
WMNF	Mixedwood (L)	MW	2018	Leaf-off	6MW2	50	1269 ± 383
WMNF	Mixedwood (L)	MW	2018	Leaf-off	6MW4	50	461 ± 126
WMNF	Mixedwood (L)	MW	2018	Leaf-off	7MW1	45	2357 ± 925
WMNF	Mixedwood (L)	MW	2018	Leaf-off	8MW2	45	568 ± 171
WMNF	Montane SF (L)	HSF	2018	Leaf-off	6HSF1	50	1785 ± 907
WMNF	Montane SF (L)	HSF	2018	Leaf-off	6HSF3	50	1419 ± 519
WMNF	Montane SF (L)	HSF	2018	Leaf-off	6HSF4	50	1117 ± 471
WMNF	Montane SF (L)	KM	2018	Leaf-off	6KM1	50	795 ± 361
WMNF	Montane SF (L)	KM	2018	Leaf-off	6KM2	45	2570 ± 560
WMNF	Montane SF (L)	SFW	2018	Leaf-off	6SFW1	50	3173 ± 1118
WMNF	Montane SF (L)	SFW	2018	Leaf-off	6SFW3	50	3101 ± 589
WMNF	Montane SF (L)	SFW	2018	Leaf-off	6SFW5	50	1506 ± 419
WMNF	Montane SF (L)	HSF	2018	Leaf-off	7HSF1	50	827 ± 242
WMNF	Montane SF (L)	SFW	2018	Leaf-off	7SFW1	50	2008 ± 905

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[c] The total number of plots/stand.

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Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
WMNF	Montane SF (L)	SFW	2018	Leaf-off	7SFW2	45	339 ± 136
WMNF	Montane SF (L)	SFW	2018	Leaf-off	7SFW3	45	728 ± 305
NB	Lowland SF (E)	SFU	2015	Leaf-on	0SFU1	49	10285 ± 3473
NB	Lowland SF (E)	SFF	2015	Leaf-on	9SFF1	47	3303 ± 2370
NB	Lowland SF (E)	SFF	2015	Leaf-on	9SFF2	50	3568 ± 2253
NB	Lowland SF (E)	SFF	2015	Leaf-on	9SFF3	49	3203 ± 675
NB	Lowland SF (E)	SFF	2015	Leaf-on	9SFF5	50	3050 ± 1005
NB	Lowland SF (E)	SFF	2015	Leaf-on	9SFF6	49	12613 ± 3388
NB	Lowland SF (E)	SFU	2015	Leaf-on	9SFU1	48	2032 ± 715
NB	Lowland SF (E)	SFU	2015	Leaf-on	9SFU3	48	4758 ± 1414
NB	Lowland SF (E)	SFU	2015	Leaf-on	9SFU4	50	4559 ± 1459
NB	Lowland SF (E)	SFU	2015	Leaf-on	9SFU5	50	3178 ± 975
NB	Mixedwood (L)	SFNH	2015	Leaf-on	0SFNH1	49	0 ± 0
NB	Hardwood (E)	NHF	2016	Leaf-on	9NHF1	50	1001 ± 209
NB	Hardwood (E)	NHF	2016	Leaf-on	9NHF2	50	924 ± 234
NB	Lowland SF (E)	SFU	2016	Leaf-on	0SFU1	49	4916 ± 944
NB	Lowland SF (E)	SFF	2016	Leaf-on	9SFF1	47	1876 ± 581
NB	Lowland SF (E)	SFF	2016	Leaf-on	9SFF2	50	3850 ± 1225
NB	Lowland SF (E)	SFF	2016	Leaf-on	9SFF3	49	2950 ± 712
NB	Lowland SF (E)	SFF	2016	Leaf-on	9SFF4	50	891 ± 211
NB	Lowland SF (E)	SFF	2016	Leaf-on	9SFF5	50	2652 ± 862
NB	Lowland SF (E)	SFF	2016	Leaf-on	9SFF6	49	14246 ± 3145
NB	Lowland SF (E)	SFU	2016	Leaf-on	9SFU1	48	2430 ± 550
NB	Lowland SF (E)	SFU	2016	Leaf-on	9SFU2	50	1023 ± 238
NB	Lowland SF (E)	SFU	2016	Leaf-on	9SFU3	45	1743 ± 539
NB	Lowland SF (E)	SFU	2016	Leaf-on	9SFU4	50	2982 ± 702
NB	Lowland SF (E)	SFU	2016	Leaf-on	9SFU5	50	1110 ± 254
NB	Mixedwood (L)	SFNH	2016	Leaf-on	0SFNH1	49	209 ± 107
NB	Mixedwood (L)	SFNH	2016	Leaf-on	0SFNH2	50	1104 ± 287
NB	Mixedwood (L)	SFNH	2016	Leaf-on	0SFNH3	50	41 ± 41
NB	Hardwood (E)	NHF	2017	Leaf-on	9NHF1	50	592 ± 249
NB	Hardwood (E)	NHF	2017	Leaf-on	9NHF2	50	1031 ± 521
NB	Lowland SF (E)	SFU	2017	Leaf-on	0SFU1	49	1883 ± 569
NB	Lowland SF (E)	SFF	2017	Leaf-on	9SFF1	44	1694 ± 641
NB	Lowland SF (E)	SFF	2017	Leaf-on	9SFF2	47	602 ± 226
NB	Lowland SF (E)	SFF	2017	Leaf-on	9SFF3	48	1354 ± 567
NB	Lowland SF (E)	SFF	2017	Leaf-on	9SFF4	49	2646 ± 1095
NB	Lowland SF (E)	SFF	2017	Leaf-on	9SFF5	49	817 ± 212

[a] Montane (≥823 m) and lowland (<823 m) classifications were based on the New Hampshire Wildlife Action Plan classification system (WAP, 2015). E = early seral (25–60 yrs. old). L = late seral (89–295 yrs. old).

[b] Sub-stand classification based on (Sperduto & Nichols, 2012).

[c] The total number of plots/stand.

Table A2 (continued). Mean (± SE) pellets/ha/month for 6 stand types, 12 sub-stand types, and individual stands (Stand id) established in 2014 (WMNF), 2015 (NB), and 2017 (CL) and resampled during spring and fall to index leaf-off (16 October–15 May) and leaf-on (16 May–15 October) density, respectively.

Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
NB	Lowland SF (E)	SFF	2017	Leaf-on	9SFF6	48	4501 ± 2206
NB	Lowland SF (E)	SFU	2017	Leaf-on	9SFU1	47	1500 ± 550
NB	Lowland SF (E)	SFU	2017	Leaf-on	9SFU2	50	172 ± 103
NB	Lowland SF (E)	SFU	2017	Leaf-on	9SFU3	48	2786 ± 885
NB	Lowland SF (E)	SFU	2017	Leaf-on	9SFU4	49	1336 ± 883
NB	Lowland SF (E)	SFU	2017	Leaf-on	9SFU5	50	3300 ± 1395
NB	Hardwood (E)	NHF	2018	Leaf-on	9NHF1	50	121 ± 89
NB	Hardwood (E)	NHF	2018	Leaf-on	9NHF2	50	222 ± 131
NB	Lowland SF (E)	SFU	2018	Leaf-on	0SFU1	49	1847 ± 726
NB	Lowland SF (E)	SFF	2018	Leaf-on	9SFF1	47	913 ± 320
NB	Lowland SF (E)	SFF	2018	Leaf-on	9SFF2	50	1941 ± 1275
NB	Lowland SF (E)	SFF	2018	Leaf-on	9SFF3	49	3549 ± 1065
NB	Lowland SF (E)	SFF	2018	Leaf-on	9SFF4	50	2269 ± 637
NB	Lowland SF (E)	SFF	2018	Leaf-on	9SFF5	50	1749 ± 588
NB	Lowland SF (E)	SFF	2018	Leaf-on	9SFF6	49	1950 ± 487
NB	Lowland SF (E)	SFU	2018	Leaf-on	9SFU1	48	1650 ± 404
NB	Lowland SF (E)	SFU	2018	Leaf-on	9SFU2	50	1050 ± 249
NB	Lowland SF (E)	SFU	2018	Leaf-on	9SFU3	48	1454 ± 414
NB	Lowland SF (E)	SFU	2018	Leaf-on	9SFU4	50	1396 ± 380
NB	Lowland SF (E)	SFU	2018	Leaf-on	9SFU5	50	3876 ± 1541
NB	Hardwood (E)	NHF	2016	Leaf-off	9NHF1	50	1042 ± 298
NB	Hardwood (E)	NHF	2016	Leaf-off	9NHF2	50	984 ± 390
NB	Lowland SF (E)	SFU	2016	Leaf-off	0SFU1	49	3349 ± 554
NB	Lowland SF (E)	SFF	2016	Leaf-off	9SFF1	46	4219 ± 665
NB	Lowland SF (E)	SFF	2016	Leaf-off	9SFF2	50	2227 ± 625
NB	Lowland SF (E)	SFF	2016	Leaf-off	9SFF3	49	7761 ± 1213
NB	Lowland SF (E)	SFF	2016	Leaf-off	9SFF4	50	4961 ± 1064
NB	Lowland SF (E)	SFF	2016	Leaf-off	9SFF5	50	7331 ± 1255
NB	Lowland SF (E)	SFF	2016	Leaf-off	9SFF6	49	11233 ± 2015
NB	Lowland SF (E)	SFU	2016	Leaf-off	9SFU1	48	3913 ± 684
NB	Lowland SF (E)	SFU	2016	Leaf-off	9SFU2	50	4294 ± 1224
NB	Lowland SF (E)	SFU	2016	Leaf-off	9SFU3	48	8538 ± 2309
NB	Lowland SF (E)	SFU	2016	Leaf-off	9SFU4	50	4221 ± 648
NB	Lowland SF (E)	SFU	2016	Leaf-off	9SFU5	50	2511 ± 619
NB	Mixedwood (L)	SFNH	2016	Leaf-off	0SFNH1	49	30 ± 30
NB	Mixedwood (L)	SFNH	2016	Leaf-off	0SFNH2	50	1103 ± 406
NB	Mixedwood (L)	SFNH	2016	Leaf-off	0SFNH3	50	184 ± 76
NB	Hardwood (E)	NHF	2017	Leaf-off	9NHF1	50	115 ± 56

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[b] Sub-stand classification based on (Sperduto & Nichols, 2012).

[c] The total number of plots/stand.

Table A2 (continued). Mean (± SE) pellets/ha/month for 6 stand types, 12 sub-stand types, and individual stands (Stand id) established in 2014 (WMNF), 2015 (NB), and 2017 (CL) and resampled during spring and fall to index leaf-off (16 October–15 May) and leaf-on (16 May–15 October) density, respectively.

Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
NB	Hardwood (E)	NHF	2017	Leaf-off	9NHF2	51	650 ± 240
NB	Lowland SF (E)	SFU	2017	Leaf-off	0SFU1	49	7357 ± 1271
NB	Lowland SF (E)	SFF	2017	Leaf-off	9SFF1	45	5989 ± 1193
NB	Lowland SF (E)	SFF	2017	Leaf-off	9SFF2	48	3811 ± 1130
NB	Lowland SF (E)	SFF	2017	Leaf-off	9SFF3	48	13138 ± 3187
NB	Lowland SF (E)	SFF	2017	Leaf-off	9SFF4	50	17777 ± 6988
NB	Lowland SF (E)	SFF	2017	Leaf-off	9SFF5	49	4506 ± 871
NB	Lowland SF (E)	SFF	2017	Leaf-off	9SFF6	49	24562 ± 4052
NB	Lowland SF (E)	SFU	2017	Leaf-off	9SFU1	48	10324 ± 1443
NB	Lowland SF (E)	SFU	2017	Leaf-off	9SFU2	50	3792 ± 871
NB	Lowland SF (E)	SFU	2017	Leaf-off	9SFU3	45	5494 ± 1478
NB	Lowland SF (E)	SFU	2017	Leaf-off	9SFU4	49	4348 ± 819
NB	Lowland SF (E)	SFU	2017	Leaf-off	9SFU5	50	6544 ± 2234
NB	Mixedwood (L)	SFNH	2017	Leaf-off	0SFNH1	49	62 ± 62
NB	Mixedwood (L)	SFNH	2017	Leaf-off	0SFNH2	50	973 ± 360
NB	Mixedwood (L)	SFNH	2017	Leaf-off	0SFNH3	49	31 ± 31
NB	Hardwood (E)	NHF	2018	Leaf-off	9NHF1	50	468 ± 179
NB	Hardwood (E)	NHF	2018	Leaf-off	9NHF2	50	760 ± 252
NB	Lowland SF (E)	SFU	2018	Leaf-off	0SFU1	49	1780 ± 447
NB	Lowland SF (E)	SFF	2018	Leaf-off	9SFF1	47	9783 ± 2031
NB	Lowland SF (E)	SFF	2018	Leaf-off	9SFF2	50	8238 ± 1718
NB	Lowland SF (E)	SFF	2018	Leaf-off	9SFF3	49	12661 ± 3288
NB	Lowland SF (E)	SFF	2018	Leaf-off	9SFF4	50	11419 ± 2254
NB	Lowland SF (E)	SFF	2018	Leaf-off	9SFF5	50	2820 ± 624
NB	Lowland SF (E)	SFF	2018	Leaf-off	9SFF6	49	21965 ± 3214
NB	Lowland SF (E)	SFU	2018	Leaf-off	9SFU1	48	5786 ± 1047
NB	Lowland SF (E)	SFU	2018	Leaf-off	9SFU2	50	3506 ± 1673
NB	Lowland SF (E)	SFU	2018	Leaf-off	9SFU3	48	4037 ± 1286
NB	Lowland SF (E)	SFU	2018	Leaf-off	9SFU4	50	4152 ± 700
NB	Lowland SF (E)	SFU	2018	Leaf-off	9SFU5	50	3413 ± 929
NB	Hardwood (E)	NHF	2019	Leaf-off	9NHF1	50	27 ± 27
NB	Hardwood (E)	NHF	2019	Leaf-off	9NHF2	50	456 ± 152
NB	Lowland SF (E)	SFU	2019	Leaf-off	0SFU1	49	2847 ± 517
NB	Lowland SF (E)	SFF	2019	Leaf-off	9SFF1	47	7247 ± 1593
NB	Lowland SF (E)	SFF	2019	Leaf-off	9SFF2	50	6228 ± 1753
NB	Lowland SF (E)	SFF	2019	Leaf-off	9SFF3	49	7604 ± 1308
NB	Lowland SF (E)	SFF	2019	Leaf-off	9SFF4	50	14629 ± 2944
NB	Lowland SF (E)	SFF	2019	Leaf-off	9SFF5	50	3595 ± 682

[a] Montane (≥823 m) and lowland (<823 m) classifications were based on the New Hampshire Wildlife Action Plan classification system (WAP, 2015). E = early seral (25–60 yrs. old). L = late seral (89–295 yrs. old).

[b] Sub-stand classification based on (Sperduto & Nichols, 2012).

[c] The total number of plots/stand.

Table A2 (continued). Mean (± SE) pellets/ha/month for 6 stand types, 12 sub-stand types, and individual stands (Stand id) established in 2014 (WMNF), 2015 (NB), and 2017 (CL) and resampled during spring and fall to index leaf-off (16 October–15 May) and leaf-on (16 May–15 October) density, respectively.

Region	Stand type[a]	Sub-stand type[b]	Year	Season	Stand id	Plots[c]	Pellets/ha/month
NB	Lowland SF (E)	SFF	2019	Leaf-off	9SFF6	49	15886 ± 2970
NB	Lowland SF (E)	SFU	2019	Leaf-off	9SFU1	48	6133 ± 813
NB	Lowland SF (E)	SFU	2019	Leaf-off	9SFU2	50	5125 ± 1386
NB	Lowland SF (E)	SFU	2019	Leaf-off	9SFU3	48	6196 ± 2229
NB	Lowland SF (E)	SFU	2019	Leaf-off	9SFU4	50	7977 ± 2127
NB	Lowland SF (E)	SFU	2019	Leaf-off	9SFU5	50	4939 ± 1316
CL	Lowland SF (E)	SF	2018	Leaf-on	0SF1	45	387 ± 143
CL	Lowland SF (E)	SF	2018	Leaf-on	0SF2	45	242 ± 142
CL	Lowland SF (E)	SF	2018	Leaf-on	0SF4	45	97 ± 68
CL	Lowland SF (E)	SF	2018	Leaf-on	0SF5	45	242 ± 103
CL	Lowland SF (E)	SF	2018	Leaf-on	9SF1	45	4171 ± 1022
CL	Lowland SF (E)	SF	2018	Leaf-on	9SF2	44	3412 ± 1420
CL	Lowland SF (E)	SF	2018	Leaf-on	9SF3	44	5821 ± 1018
CL	Lowland SF (E)	SF	2018	Leaf-on	9SF4	45	638 ± 229
CL	Lowland SF (E)	SF	2018	Leaf-on	9SF6	45	2176 ± 583
CL	Lowland SF (E)	SF	2018	Leaf-on	9SF8	45	1865 ± 530
CL	Lowland SF (E)	SF	2018	Leaf-on	9SF9	45	4760 ± 879
CL	Lowland SF (E)	SF	2018	Leaf-off	0SF1	45	460 ± 232
CL	Lowland SF (E)	SF	2018	Leaf-off	0SF2	45	1199 ± 418
CL	Lowland SF (E)	SF	2018	Leaf-off	0SF4	45	189 ± 73
CL	Lowland SF (E)	SF	2018	Leaf-off	0SF5	45	1872 ± 873
CL	Lowland SF (E)	SF	2018	Leaf-off	9SF1	45	10829 ± 2025
CL	Lowland SF (E)	SF	2018	Leaf-off	9SF2	45	7026 ± 1559
CL	Lowland SF (E)	SF	2018	Leaf-off	9SF3	45	14874 ± 2499
CL	Lowland SF (E)	SF	2018	Leaf-off	9SF4	45	2335 ± 527
CL	Lowland SF (E)	SF	2018	Leaf-off	9SF6	45	7764 ± 1791
CL	Lowland SF (E)	SF	2018	Leaf-off	9SF8	45	21974 ± 4599
CL	Lowland SF (E)	SF	2018	Leaf-off	9SF9	45	15087 ± 1786
CL	Lowland SF (E)	SF	2019	Leaf-off	0SF1	45	86 ± 48
CL	Lowland SF (E)	SF	2019	Leaf-off	0SF2	45	715 ± 251
CL	Lowland SF (E)	SF	2019	Leaf-off	0SF4	45	29 ± 29
CL	Lowland SF (E)	SF	2019	Leaf-off	0SF5	45	614 ± 203
CL	Lowland SF (E)	SF	2019	Leaf-off	9SF1	45	2946 ± 644
CL	Lowland SF (E)	SF	2019	Leaf-off	9SF2	45	5988 ± 2270
CL	Lowland SF (E)	SF	2019	Leaf-off	9SF3	45	12443 ± 1704
CL	Lowland SF (E)	SF	2019	Leaf-off	9SF4	45	1259 ± 420
CL	Lowland SF (E)	SF	2019	Leaf-off	9SF6	45	5149 ± 1628
CL	Lowland SF (E)	SF	2019	Leaf-off	9SF8	45	11884 ± 2510
CL	Lowland SF (E)	SF	2019	Leaf-off	9SF9	45	20996 ± 2634

[a] Montane (≥823 m) and lowland (<823 m) classifications were based on the New Hampshire Wildlife Action Plan classification system (WAP, 2015). E = early seral (25–60 yrs. old). L = late seral (89–295 yrs. old). [b] Sub-stand classification based on (Sperduto & Nichols, 2012). [c] The total number of plots/stand.

Table A3. Mean (± SE) leaf-off pellet density (pellets/ha/month) for 1 m^2 plots vs. spatial capture-recapture (SCR) density estimates (hares/ha) sampled within the same stands from 7 May–13 August 2016.

Region	Stand	pellets/ha/month	Density (Hares/ha)
NB	9NHF2	984 ± 390	0.20 (0.04–0.92)
NB	9SFF3	7761 ± 1213	0.57 (0.25–1.27)
NB	9SFF6	11233 ± 2015	0.55 (0.22–1.35)
NB	0SFU1	3349 ± 554	0.54 (0.23–1.28)
NB	9SFU2	4294 ± 1224	0.30 (0.11–0.81)
WMNF	6HD2	27 ± 27	0 (0–0)
WMNF	6HSF3	1986 ± 636	0.25 (0.08–0.72)
WMNF	6KM1	523 ± 230	0.22 (0.05–1.00)
WMNF	6LSF1	1029 ± 281	0.15 (0.04–0.54)
WMNF	6LSF3	2174 ± 824	0.09 (0.01–0.71)
WMNF	6MW4	966 ± 311	0.27 (0.08–0.99)

Table A4. Summary of negative binomial generalized linear mixed model (GLMM) evaluating differences in relative hare density (pellets/m^2/day) between stand types. The output includes the estimated difference between stand types, standard error, degrees of freedom, T-ratio, and Tukey's *P*-value. Significant differences (P <0.05) between regions are highlighted in bold.

Contrast	Estimate	SE	DF	T-ratio	*P*-value
early hardwood - early lowland softwood	**-2.479**	**0.71**	**9356**	**-3.492**	**0.0064**
early hardwood - late hardwood	**3.12**	**1.096**	**9356**	**2.847**	**0.0504**
early hardwood - late lowland softwood	-1.023	1.007	9356	-1.016	0.9127
early hardwood - late mixedwood	-0.614	0.971	9356	-0.632	0.9886
early hardwood - late montane softwood	-0.457	0.966	9356	-0.473	0.9971
early lowland softwood - late hardwood	**5.599**	**0.862**	**9356**	**6.496**	**<.0001**
early lowland softwood - late lowland softwood	1.456	0.744	9356	1.956	0.3683
early lowland softwood - late mixedwood	1.865	0.691	9356	2.698	0.0758
early lowland softwood - late montane softwood	**2.022**	**0.689**	**9356**	**2.935**	**0.0392**
late hardwood - late lowland softwood	**-4.144**	**0.689**	**9356**	**-6.016**	**<.0001**
late hardwood - late mixedwood	**-3.734**	**0.669**	**9356**	**-5.58**	**<.0001**
late hardwood - late montane softwood	**-3.577**	**0.611**	**9356**	**-5.856**	**<.0001**
late lowland softwood - late mixedwood	0.41	0.515	9356	0.796	0.9683
late lowland softwood - late montane softwood	0.566	0.461	9356	1.228	0.8231
late mixedwood - late montane softwood	0.157	0.428	9356	0.366	0.9991

Table A5. Summary of negative binomial generalized linear mixed model (GLMM) evaluating differences in relative hare density (pellets/m^2/day) between regions. The output includes the estimated difference between regions, standard error, degrees of freedom, T-ratio, and Tukey's *P*-value. Significant differences (P <0.05) between regions are highlighted in bold.

Contrast	Estimate	SE	DF	T-ratio	*P*-value
CL - NB	-0.39	0.466	7647	-0.837	0.6802
CL - WMNF	**1.19**	**0.432**	**7647**	**2.749**	**0.0165**
NB - WMNF	**1.58**	**0.397**	**7647**	**3.971**	**0.0002**

Table A6. Summary of negative binomial generalized linear mixed model (GLMM) evaluating differences in relative hare density (pellets/m^2/day) between years for each region. The output includes the estimated difference between years, standard error, degrees of freedom, T-ratio, and Tukey's *P*-value. Significant differences (*P* <0.05) between years are highlighted in bold.

Region	Contrast	Estimate	SE	DF	T-ratio	*P*-value
WMNF	2015 spring – 2016 spring	-0.0099	0.0996	3912	-0.1	0.9996
	2015 spring – 2017 spring	**0.2855**	**0.1024**	**3912**	**2.787**	**0.0274**
	2015 spring – 2018 spring	-0.0451	0.1020	3912	-0.442	0.9712
	2016 spring – 2017 spring	**0.2955**	**0.0980**	**3912**	**3.016**	**0.0137**
	2016 spring – 2018 spring	-0.0351	0.0971	3912	-0.361	0.9839
	2017 spring – 2018 spring	**-0.3305**	**0.0982**	**3912**	**-3.364**	**0.0043**
NB	**2016 spring – 2017 spring**	**-0.2518**	**0.0673**	**2742**	**-3.739**	**0.0011**
	2016 spring – 2018 spring	-0.0412	0.0683	2742	-0.603	0.9312
	2016 spring – 2019 spring	-0.0529	0.0683	2742	-0.774	0.8663
	2017 spring – 2018 spring	**0.2106**	**0.0659**	**2742**	**3.197**	**0.0077**
	2017 spring – 2019 spring	**0.1990**	**0.0657**	**2742**	**3.026**	**0.0133**
	2018 spring – 2019 spring	-0.0117	0.0661	2742	-0.177	0.998
CL	**2018 spring – 2019 spring**	**0.4370**	**0.0776**	**977**	**5.638**	**<0.0001**

Table A7. Parameter estimates, standard errors (SE), Wald's z-values, and probability statistics for landscape-scale density model evaluating differences between the NB and WMNF. Note, NB is the reference category for all comparisons.

Parameter	Estimate	SE	z	P(>|z|)
p0.(Intercept)	-2.858	0.314	-9.097	0.000
p0.male	-1.489	0.430	-3.466	0.001
p0.WMNF	-0.970	0.480	-2.022	0.043
p.behav	1.447	0.472	3.064	0.002
sig.(Intercept)	-2.396	0.144	-16.650	0.000
sig.WMNF	0.604	0.290	2.081	0.037
d0.(Intercept)	-2.048	0.301	-6.793	0.000
d.beta.WMNF	-1.604	0.572	-2.802	0.005
psi.constant	1.052	0.403	2.609	0.009

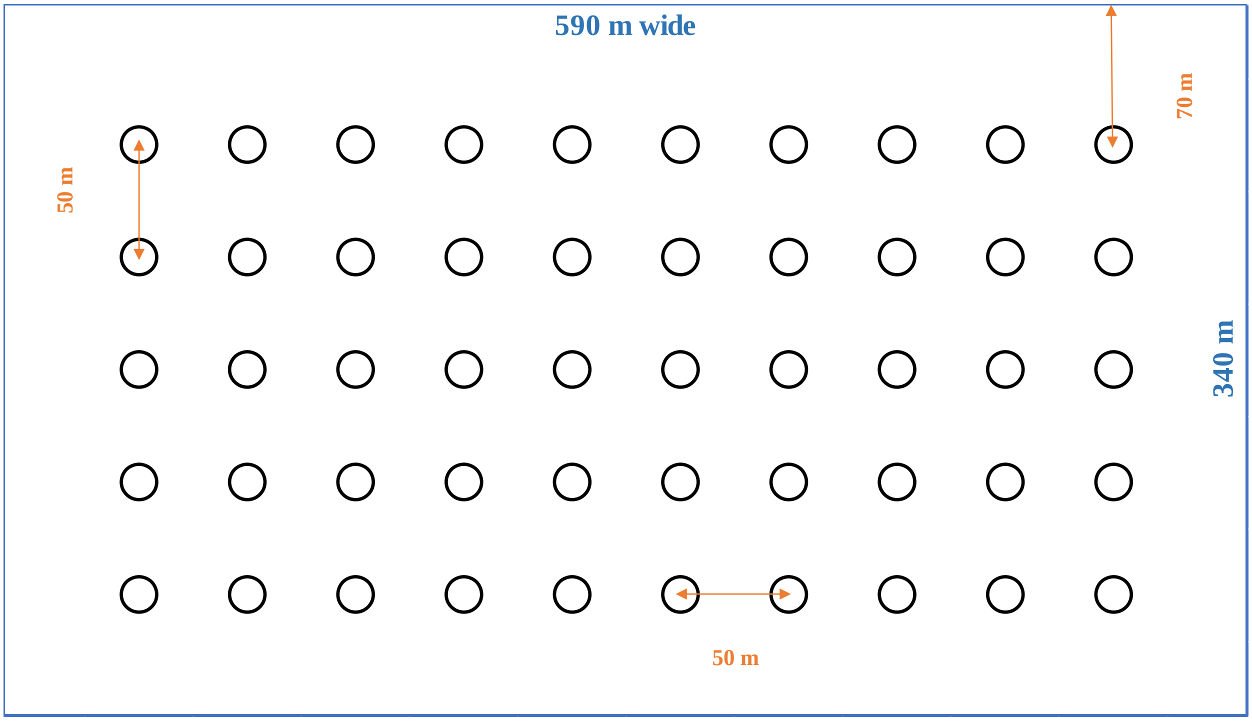

Figure A1. Schematic of a 20 ha (590 m x 340 m) 50 plot stand, where distance between plots and transects are 50 m and the buffer are 70 m. The 18 ha (540 m x 340 m) 45 plot stands contain one less row of plots.

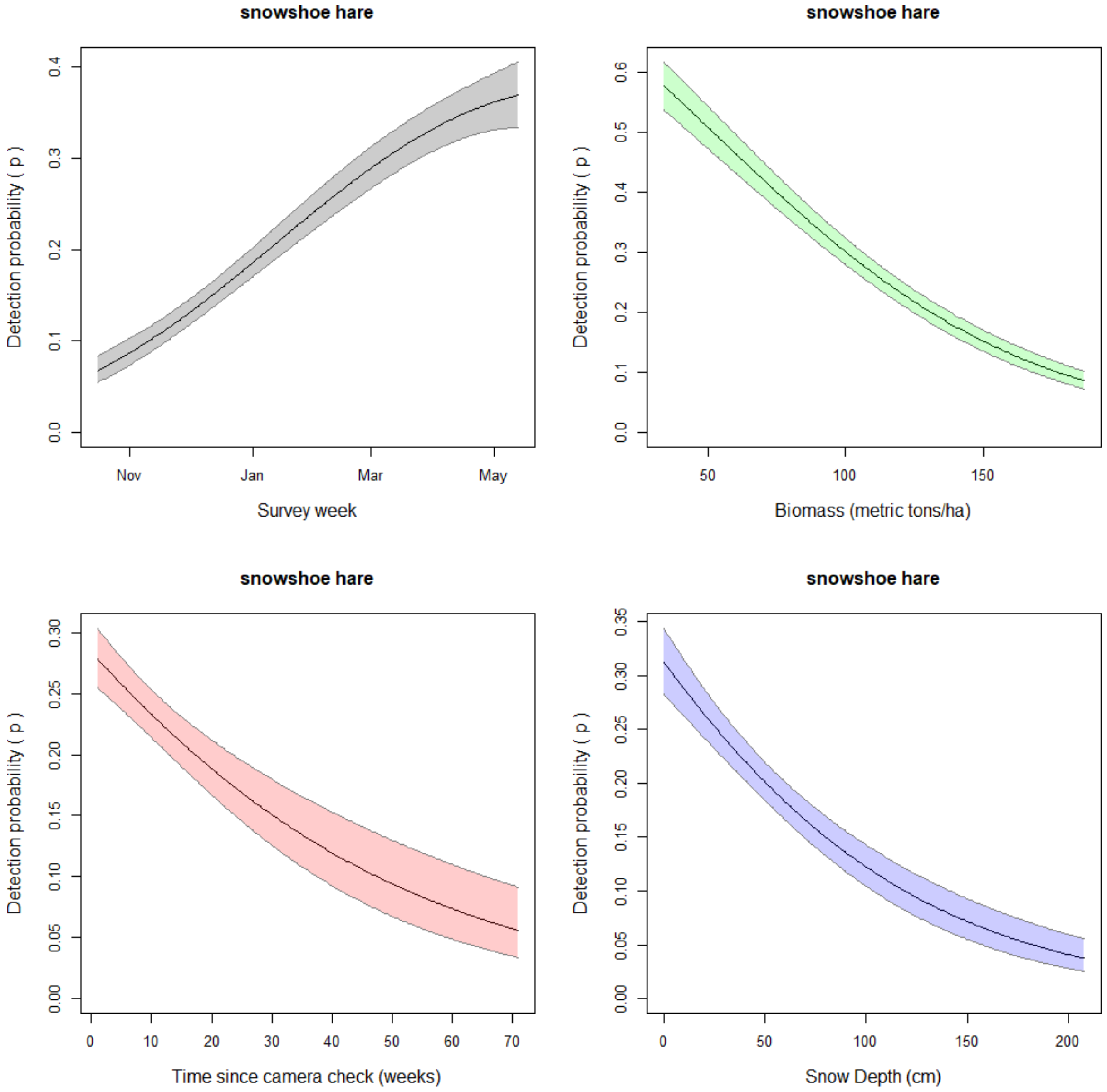

Figure A2. Covariates from top performing detection probability (*p*) models of snowshoe hares from camera surveys conducted from 9 January 2014–12 July 2019 in the U.S. states of New Hampshire and Vermont.

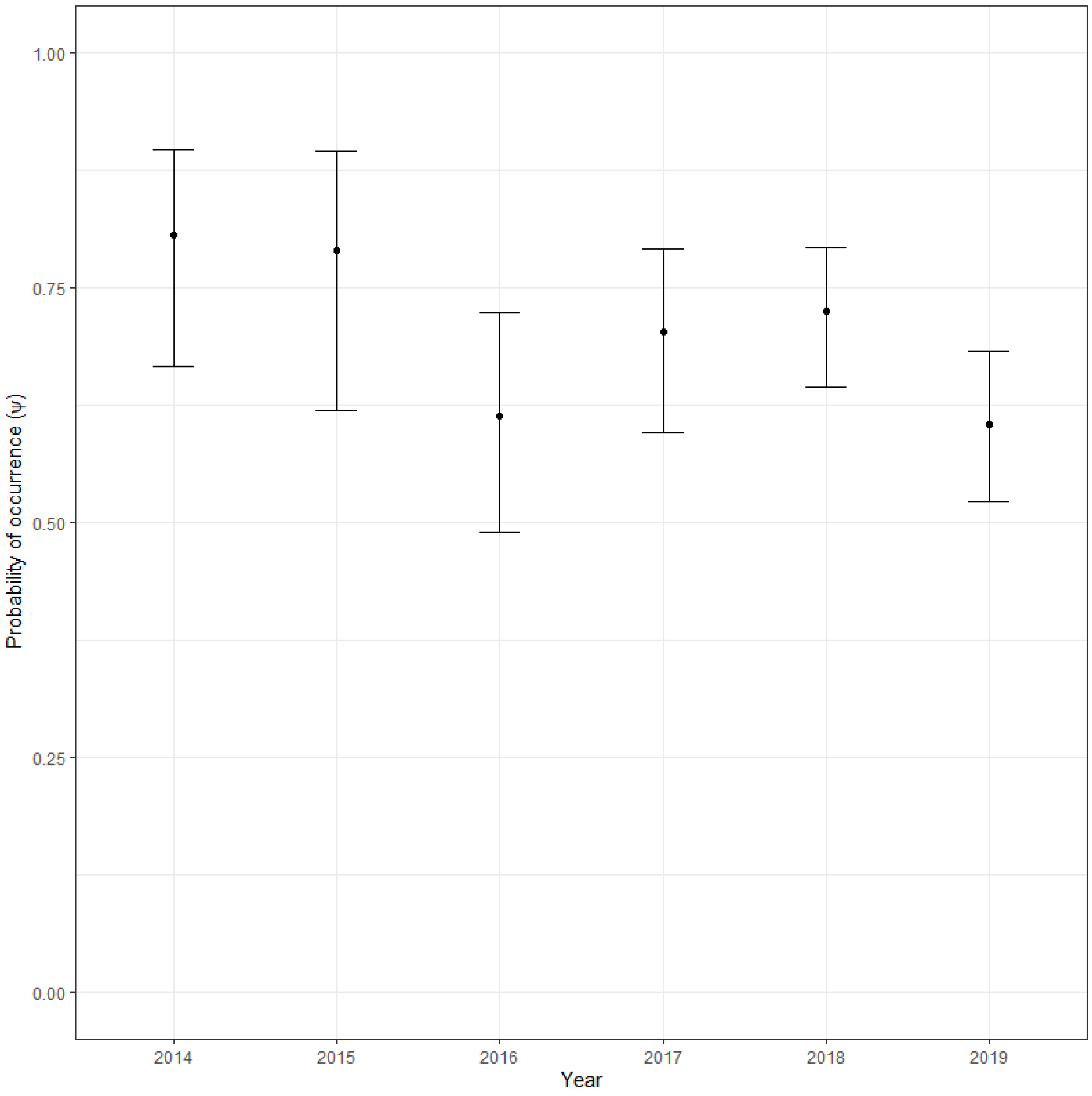

Figure A3. Variation in snowshoe hare occupancy (ψ) among sampling years from top models using camera survey data collected from 9 January 2014–12 July 2019 in New Hampshire and Vermont, USA. **Note** that all comparisons are made with 2014, the first year of sampling.

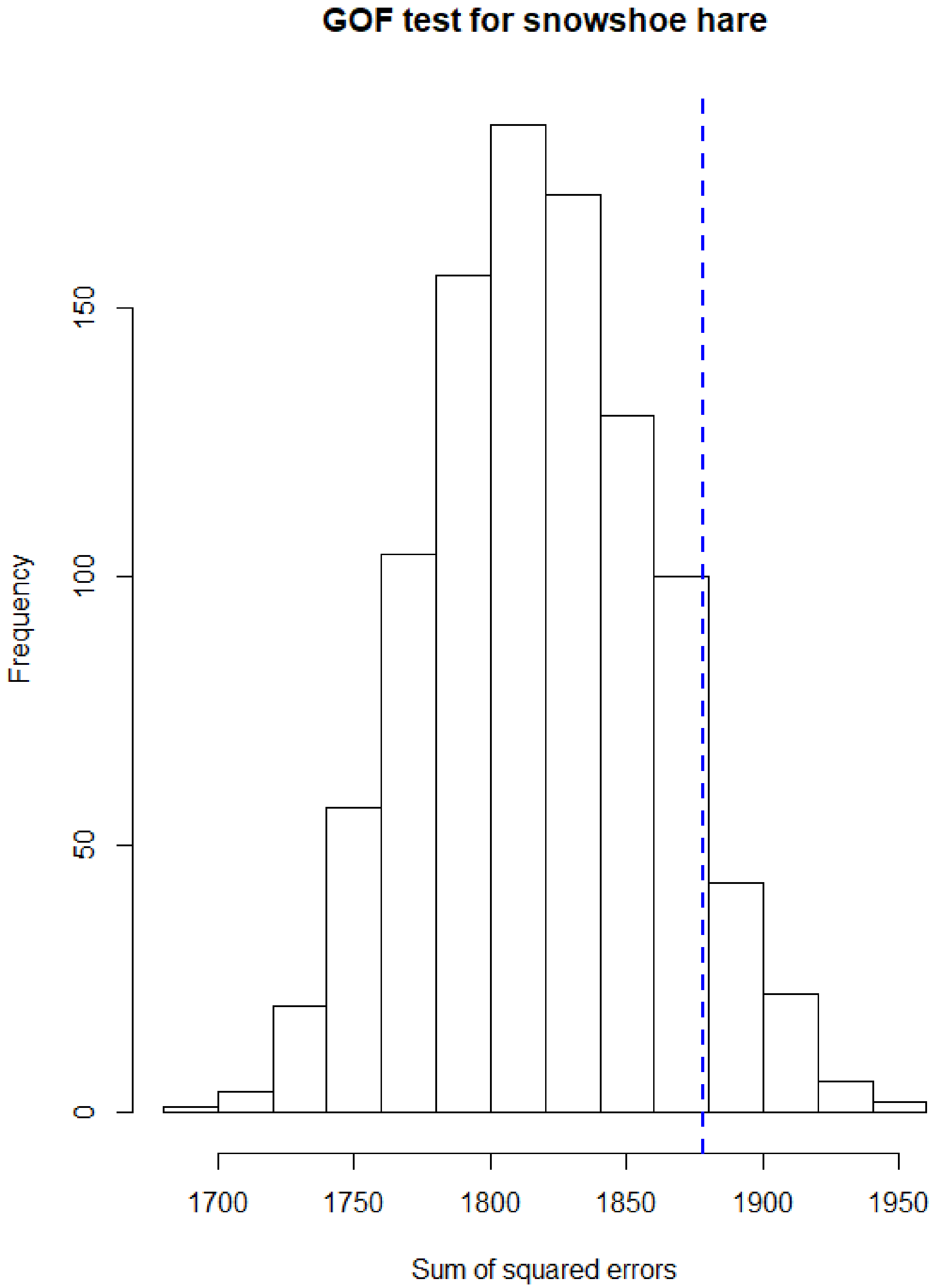

Figure A4. The sum of squared residuals (SSE) of the top snowshoe hare occupancy model (blue dashed vertical line) was within the distribution of bootstrapped SSEs, indicating good fit.

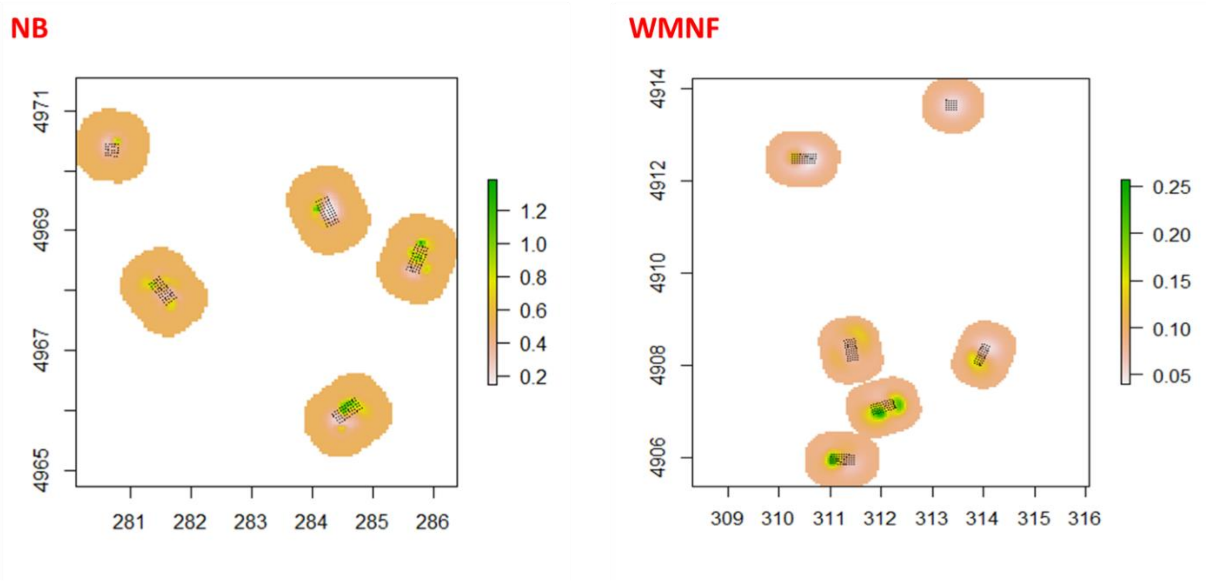

Figure A5. Landscape-scale snowshoe hare density derived from spatial capture-recapture (SCR) estimates in the NB (x̄ = 0.52 hares/ha) and WMNF (x̄ = 0.10 hares/ha). **Note**: Axes for each figure are the UTM coordinates/1,000. The color ramp for the legends are similar but values are different for the NB and WMNF.

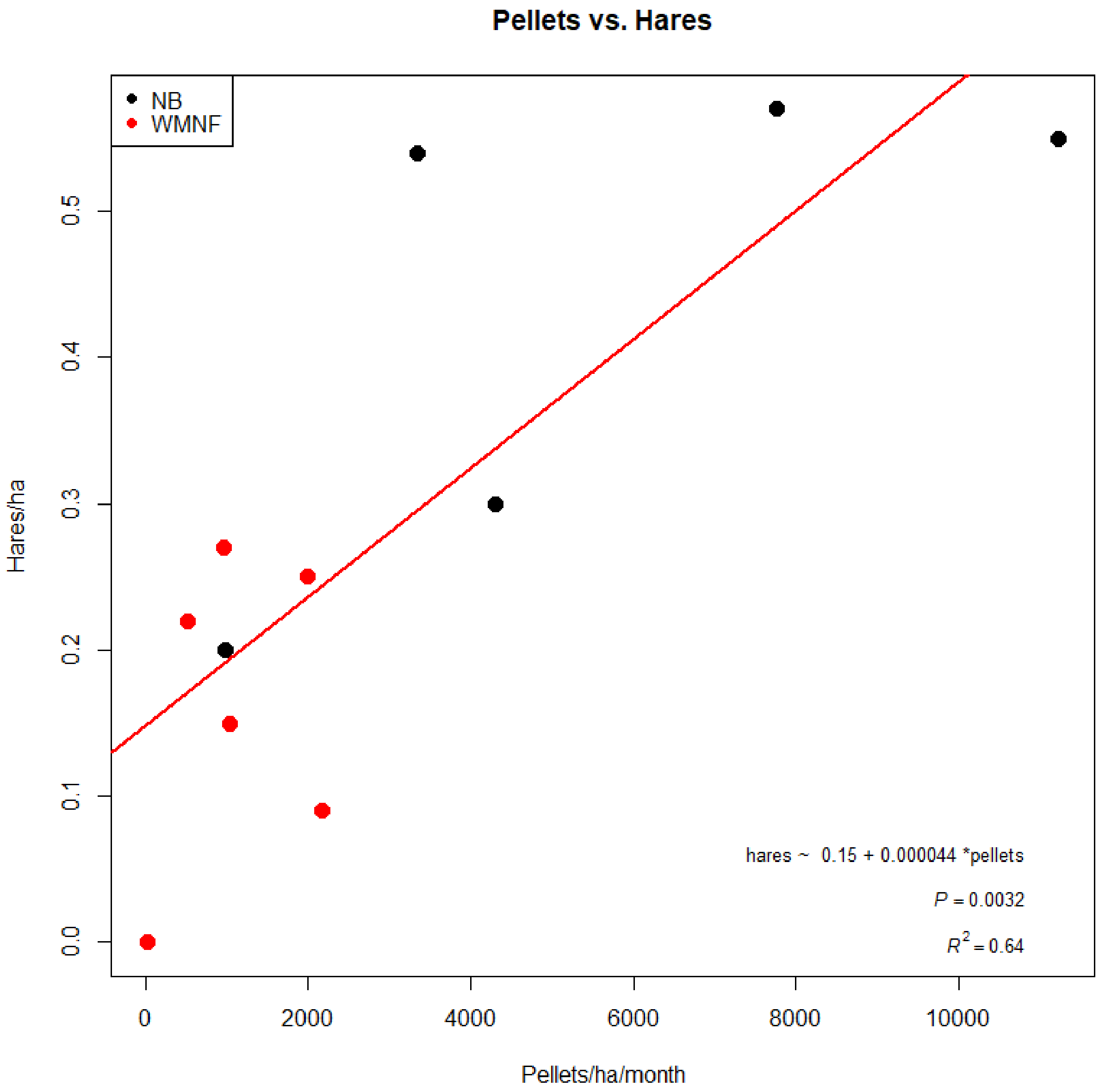

Figure A6. Relationship between pellet-plot density (pellets/ha/month) vs. hare density (hares/ha) estimated using spatial capture-recapture models. Pellets were counted (leaf-off season; 16 October 2015–15 May 2016) and hares were live-trapped (20 June–13 August 2016) in 11 stands that varied in pellet density.

References for Chapter 3 Supplemental Methods

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APPENDIX D

SUPPLEMENTAL: FORECASTING SPECIES DISTRIBUTIONS: CORRELATION DOES NOT EQUAL CAUSATION

Table A1. R packages used for running statistical analyses, creating predictive maps, and evaluating predictive performance of models.

R Package	Use	Reference[a]
PresenceAbsence	Evaluate predictive ability of models	(Freeman & Moisen, 2008)
raster	Create predictive maps from models	(Hijmans et al., 2015)
unmarked	Fitting site occupancy models	(Fiske & Chandler, 2011)
piecewiseSEM	Fitting causal models	(Lefcheck, 2016)
viridis	Color scheme for rasters	(Garnier, 2018)
lme4	Fit binomial models within *piecewiseSEM*	(Bates et al., 2015)

[a] **References**

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Garnier, S. 2018. viridis: Default Color Maps from “matplotlib.” - CRAN in press.

Hijmans, R. J. et al. 2015. Package ‘ raster .’ - https://cran.r-project.org/web/packages/raster/raster.pdf

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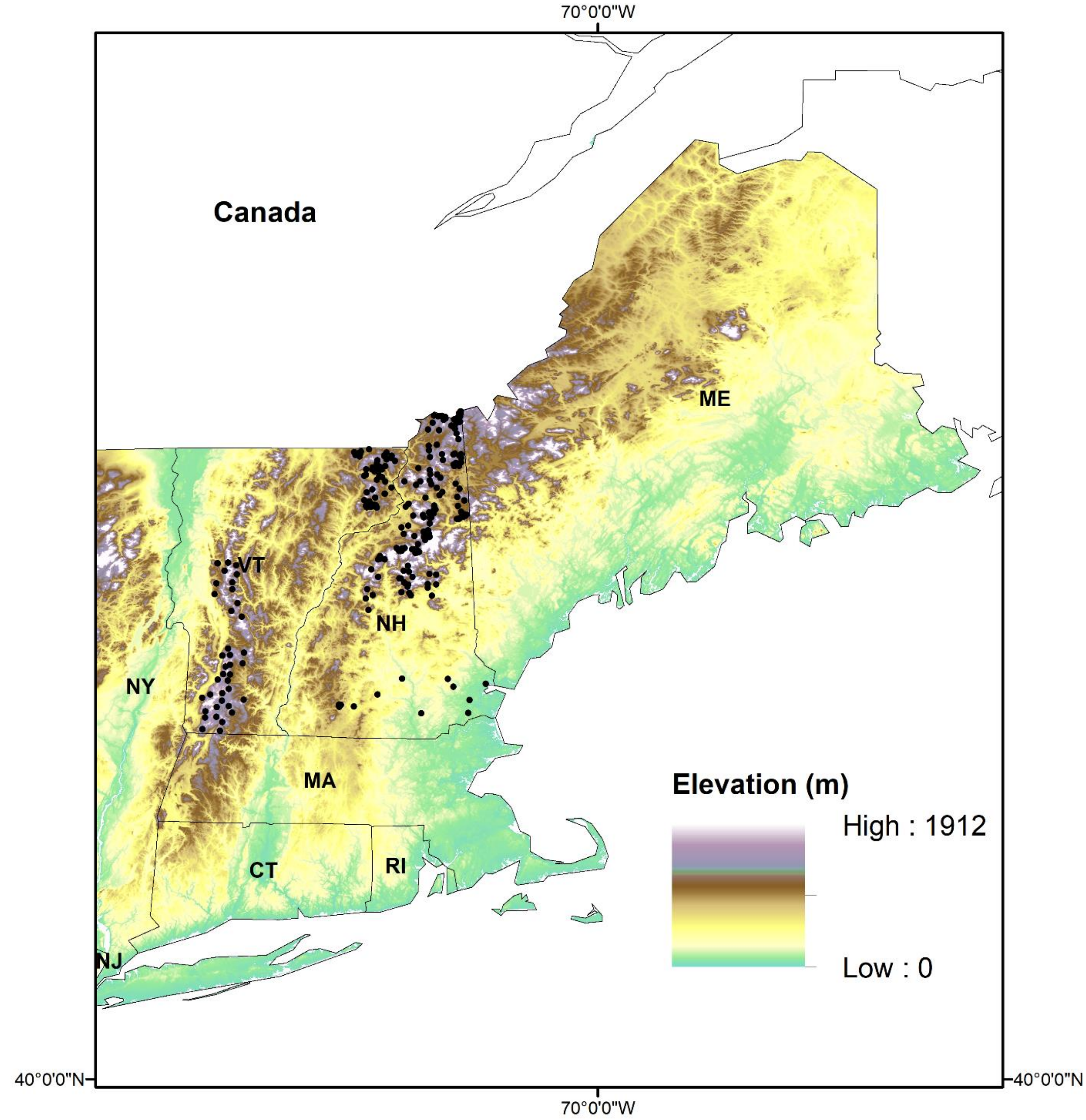

Figure A1. Region used for evaluating current and future distributions given projected changes in snow depth (mm) and forest biomass (kg/m^2). Carnivore and prey species were sampled from 2014–2019 using 257 remote cameras (black dots) distributed along latitudinal and elevation gradients.

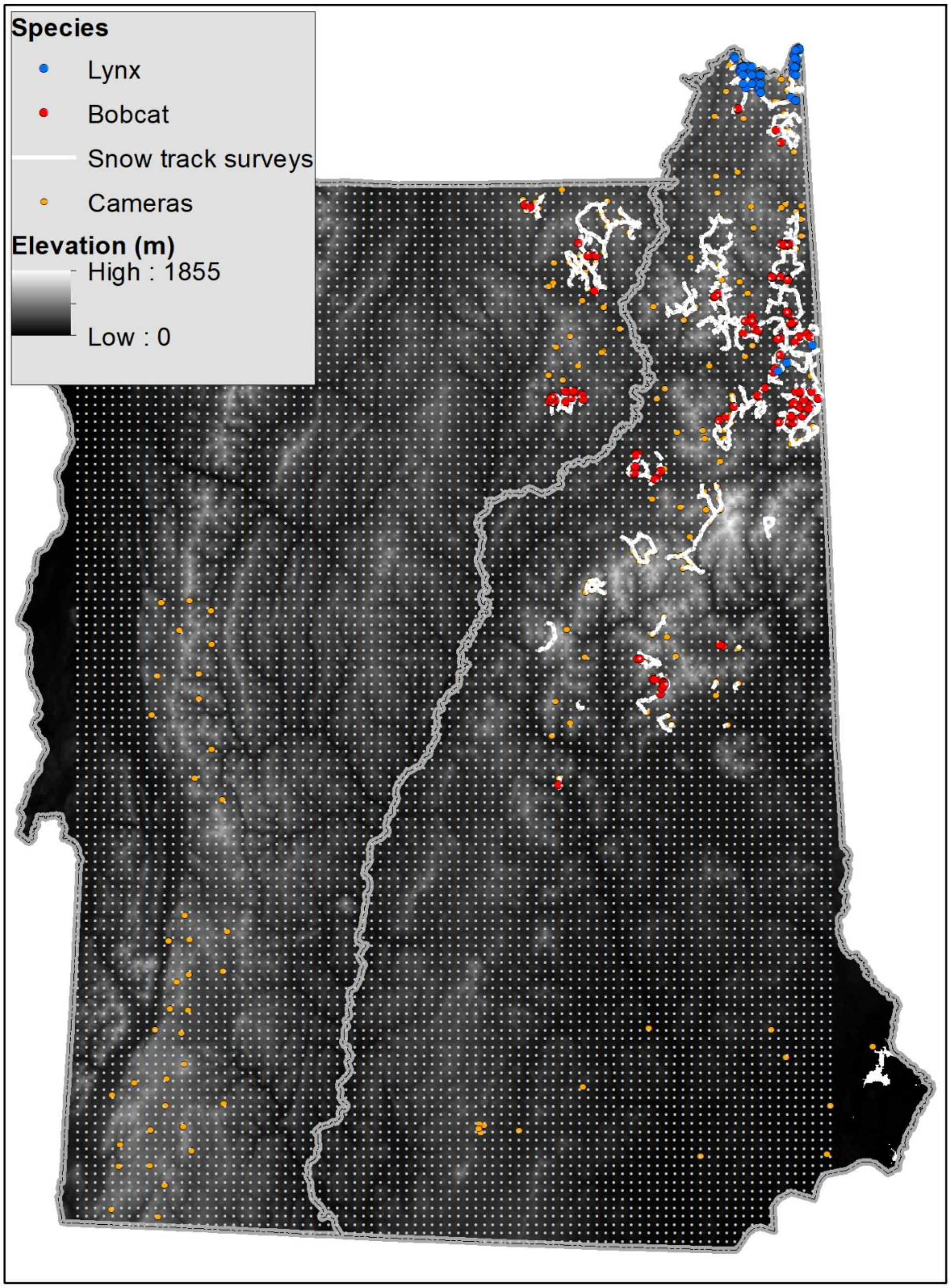

Figure A2. Independent detection data of Canada lynx (*Lynx canadensis*) and bobcats (*Lynx rufus*) collected during snow track surveys from 4 January 2014 – 28 February 2018 and verified records (lynx-only) collected by state agencies (gray points) within the same time frame.

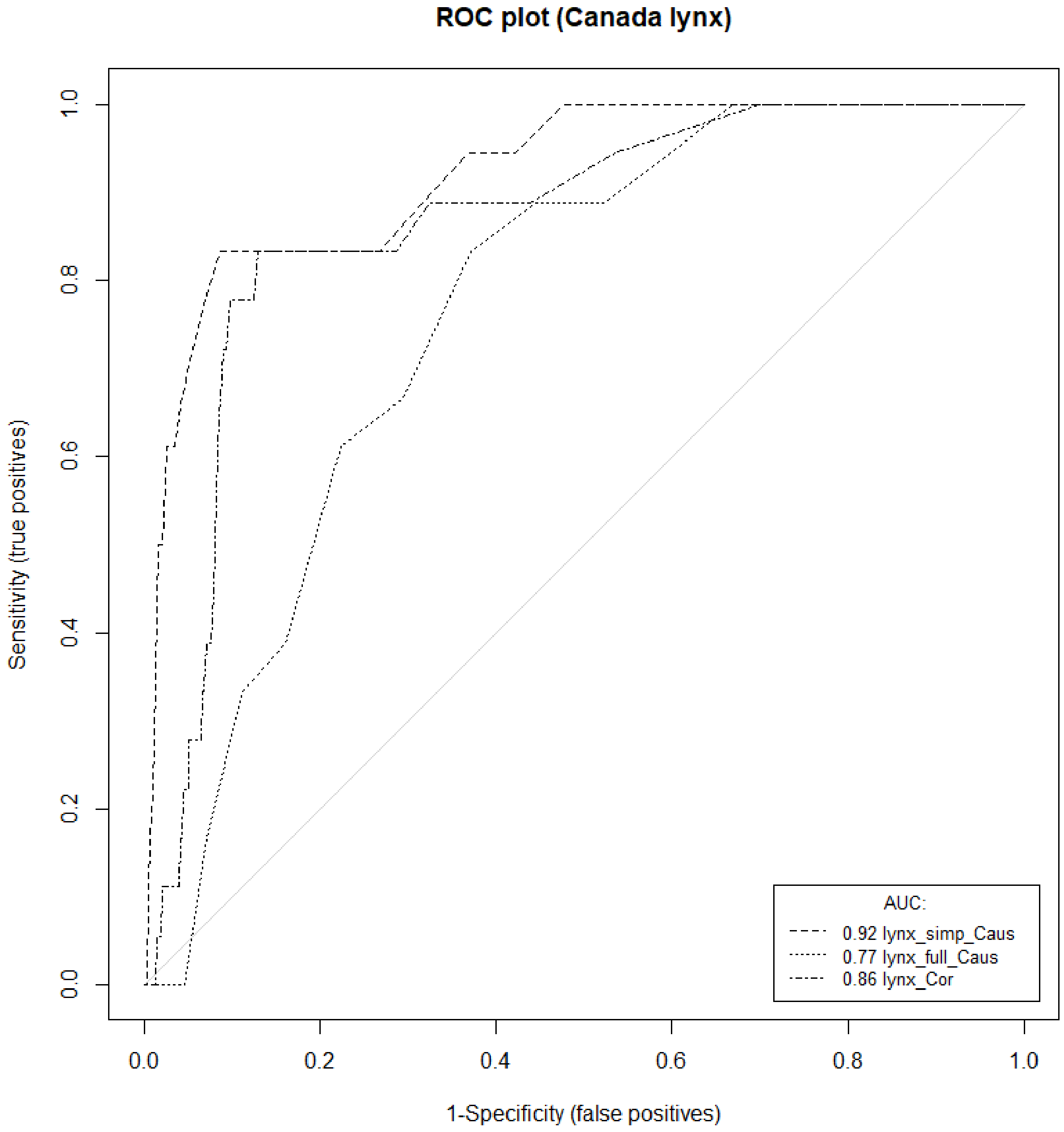

Figure A3. Receiver operating characteristic (ROC) plot with area under the ROC curve (AUC) values for Canada lynx (*Lynx canadensis*) given 3 different models.

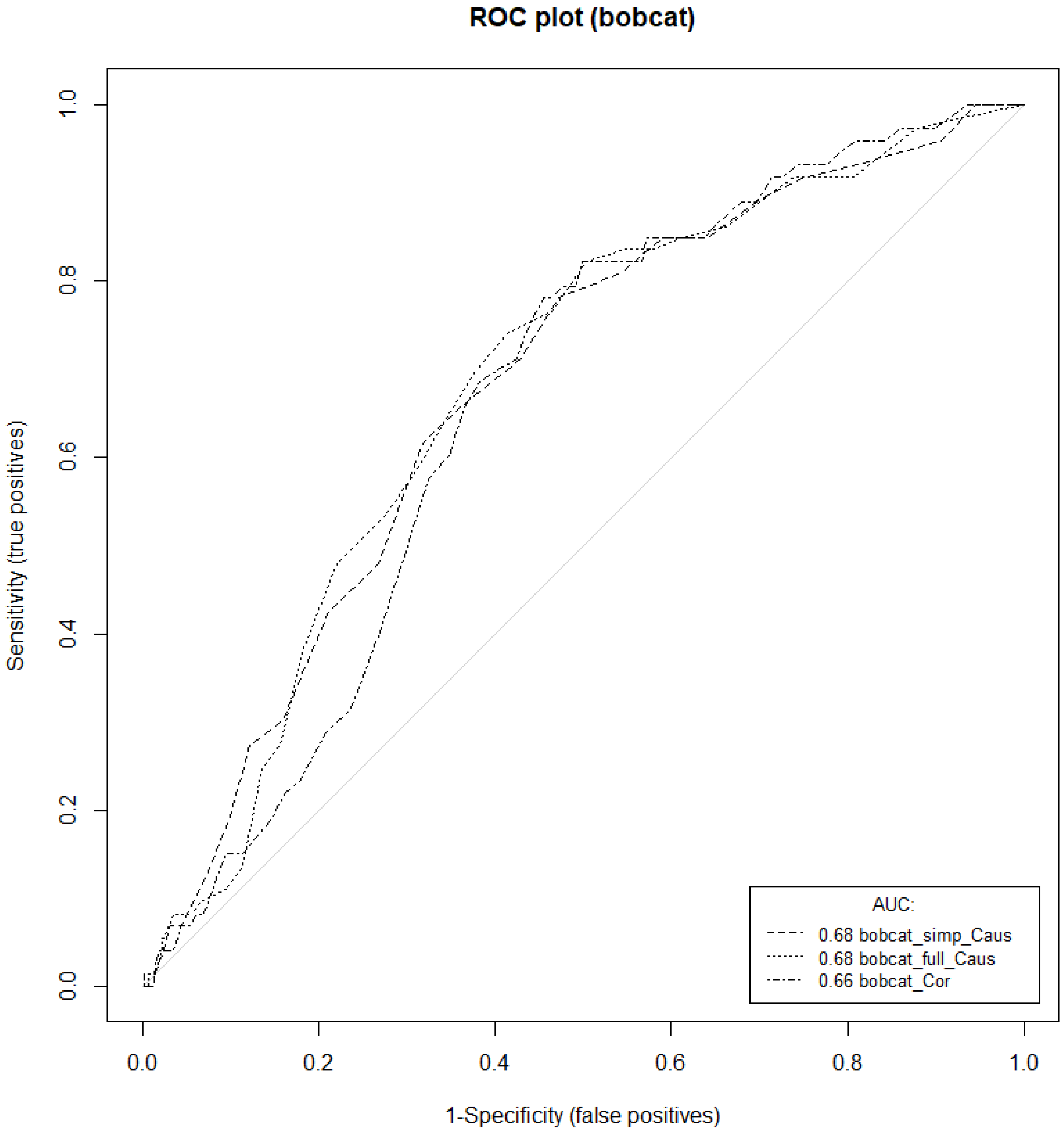

Figure A4. Receiver operating characteristic (ROC) plot with area under the ROC curve (AUC) values for bobcat (*Lynx rufus*) given 3 different models.

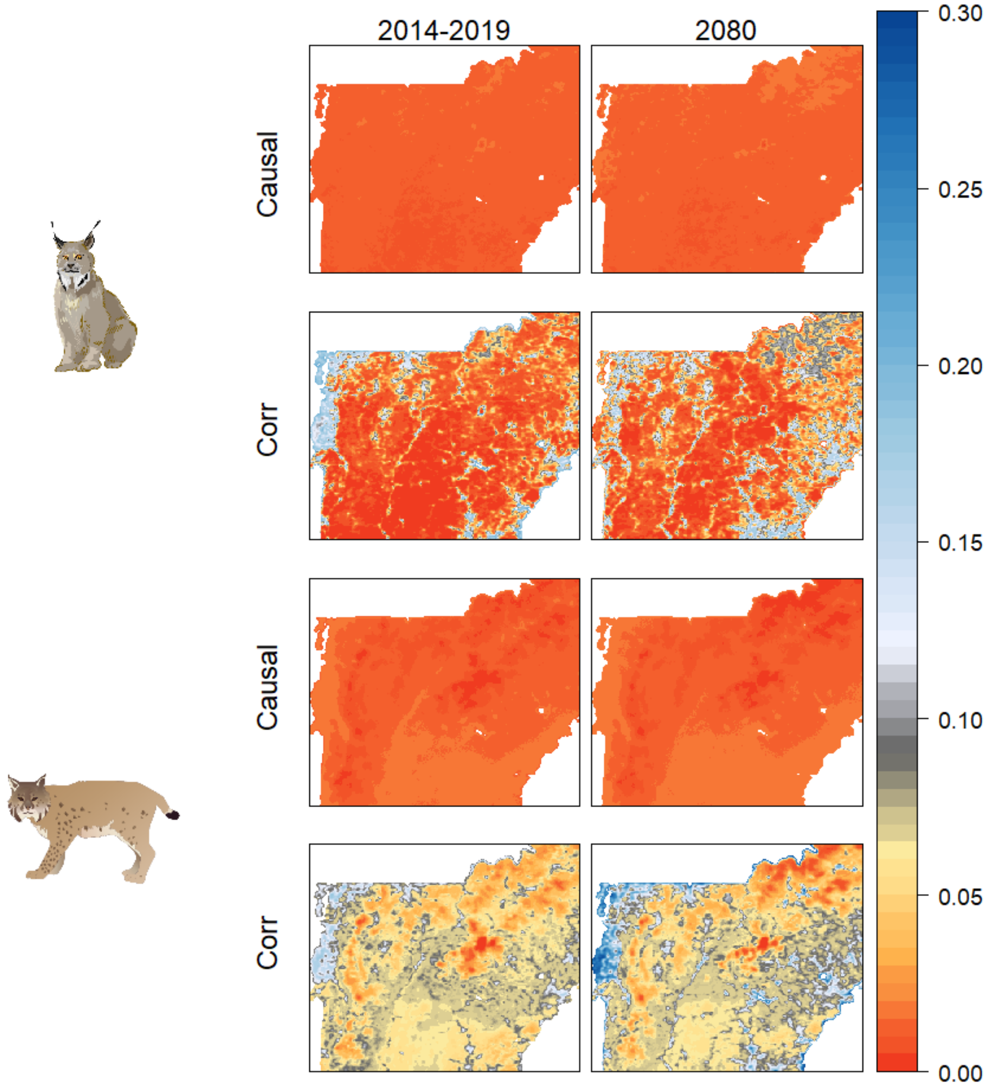

Figure A5. Spatially explicit estimates of uncertainty (standard errors) for lynx (top rows) and bobcat (bottom rows) for causal and correlative (corr) modeling approaches. Note, comparisons of uncertainty between modeling approaches are not possible because standard errors were estimated differently. However, relative comparisons can be made between modeling approaches.

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