Journal of Biogeography

WILEY

Abiotic stress and biotic factors mediate range dynamics on opposing edges

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Funding information
U.S. Department of the Interior Northeast Climate Adaptation Science Center

Handling editor: Enrique Martínez-Meyer

Abstract

Aim: In the face of global change, understanding causes of range limits are one of the most pressing needs in biogeography and ecology. A prevailing hypothesis is that abiotic stress forms cold (upper latitude/altitude) limits, whereas biotic interactions create warm (lower) limits. A new framework – Interactive Range-Limit Theory (iRLT) – asserts that positive biotic factors such as food availability can ameliorate abiotic stress along cold edges, whereas abiotic stress can have a positive effect and mediate biotic interactions (e.g., competition) along warm limits.

Location: Northeastern United States

Taxon: Carnivora

Methods: We evaluated two hypotheses of iRLT using occupancy and structural equation modeling (SEM) frameworks based on data collected over a 6-year period (2014–2019) of six carnivore species across a broad latitudinal (42.8–45.3°N) and altitudinal (3–1451 m) gradient.

Results: We found that snow directly limits populations, but prey or habitat availability can influence range dynamics along cold edges. For example, bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) were limited by deep snow and long winters, but the availability of prey had a strong positive effect. Conversely, snow had a strong positive effect on the warm limits of Canada lynx (*Lynx canadensis*), countering the negative effect of competition with the phylogenetically similar bobcat and with coyotes, highlighting how climate mediates competition between species.

Main conclusions: We used an integrated dataset that included competitors and prey species collected at the same spatial and temporal scale. As such, this design, along with a causal modeling framework (SEM), allowed us to evaluate community-wide hypotheses at macroecological scales and identify coarse-scale drivers of species' range limits. Our study supports iRLT and underscores the need to consider direct and indirect mechanisms for studying range dynamics and species' responses to global change.

1 | INTRODUCTION

The causes of range limits have long fascinated biogeographers and ecologists. An enduring theory postulates that harsh climate forms cold (upper latitudinal/altitudinal) boundaries and biotic interactions form warm (lower) limits (Darwin, 1859; 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, 2020).

The recently proposed 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, 2020). Positive biotic factors, such as prey or habitat availability, can ameliorate abiotic stress along cold range limits. This dynamic is well illustrated by populations that either persist or expand along cold limits, despite abiotic stress, when abundant food resources became available (Sirén & Morelli, 2020). For example, populations of southern flying squirrels (*Glaucomys volans*) along cold limits have higher survival during severe winters when food resources (i.e., tree mast) are abundant (Bowman et al., 2005). Their recent northward range expansion is attributed to milder winters, yet also fueled by masting events (Bowman et al., 2005). Conversely, abiotic stress can mediate negative biotic interactions (e.g., competition) for populations along warm limits. Indeed, many studies indicate that populations along warm limits exhibit a positive association with abiotic stress (e.g., cold temperature) that is thought to control competitors or predators (Sirén & Morelli, 2020). This is exemplified by southern populations of wolverines (*Gulo gulo*) that depend on long and snowy winters to protect their cached food supplies (Inman et al., 2012). There is strong evidence for many taxa that positive biotic and abiotic effects interact with limiting factors to form range boundaries and facilitate shifts (see review in Sirén & Morelli, 2020). Thus, iRLT extends existing theory on range limits and provides a framework for evaluating how interactions between abiotic and biotic factors form range limits and how this varies by cold and warm distributional edges.

Here, we empirically test the predictions set forth by iRLT using data from a suite of carnivores at their range limits in the boreal-temperate ecotone in the northeastern United States: the cold (upper latitudinal/altitudinal) limit of bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and fishers (*Pekania pennanti*), and the warm (lower latitudinal/altitudinal) limit of Canada lynx (*Lynx canadensis*) and American martens (*Martes americana*) (Figure 1). Previous work has shown that bobcats, coyotes, and fishers have a negative association with deep snow and a strong association with abundant or large prey in northern regions (Jensen & Humphries, 2019; Litvaitis et al., 1986; Major & Sherburne, 1987; Scully et al., 2018). Furthermore, it is widely assumed that competition limits lynx and martens along their warm-edge boundaries (Jensen & Humphries, 2019; Peers et al., 2013; Scully et al., 2018). However, it is unclear which factors 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 influence populations indirectly or directly along warm and cold edges. To this end, we used structural equation modeling (SEM) framework, which has been advocated by previous authors (e.g., Wisz et al., 2013) yet not implemented, to disentangle correlated factors that form range limits. Developing a mechanistic understanding is necessary to accurately predict, and ultimately to prepare for, climate change responses along range edges (Urban et al., 2016).

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 (Table 1, Figure 2). We included the previously mentioned carnivores as well as red fox (*Vulpes vulpes*) and three prey species (snowshoe hare, *Lepus americanus*; red squirrel, *Tamiasciurus hudsonicus*; white-tailed deer, *Odocoileus virginianus*) that have been shown to affect population and community dynamics (Table 2). Red fox were not found along or near range limits in the study region. However, we retained this species due to its potential influence on community dynamics (see Table 2). Finally, we were primarily evaluating factors influencing latitudinal limits, but some species (e.g., fisher) were at or near their altitudinal limits, resulting in lower occupancy. The expansive high-altitude region was located in the northern part of our study area (Figures 1 and 3) and had a colder and snowier climate that was more representative of the northern latitudinal limit of these species' ranges.

Our first hypothesis was that snow has a direct-limiting effect on populations along cold edges but that unlinked biotic factors (i.e., density-independent, Anderson, 2017), such as habitat or prey availability, ameliorate harsh conditions and indirectly form range limits (Table 1, Figure 2). Accordingly, we predicted that snow would have a negative and direct effect for carnivore populations along cold edges, whereas increased prey and habitat availability would have positive direct and indirect effects, respectively (Table 2, Figure 2). For populations along warm-edge limits, we hypothesized that snow mediates competitive interactions between phylogenetically and ecologically similar species and ultimately affects range
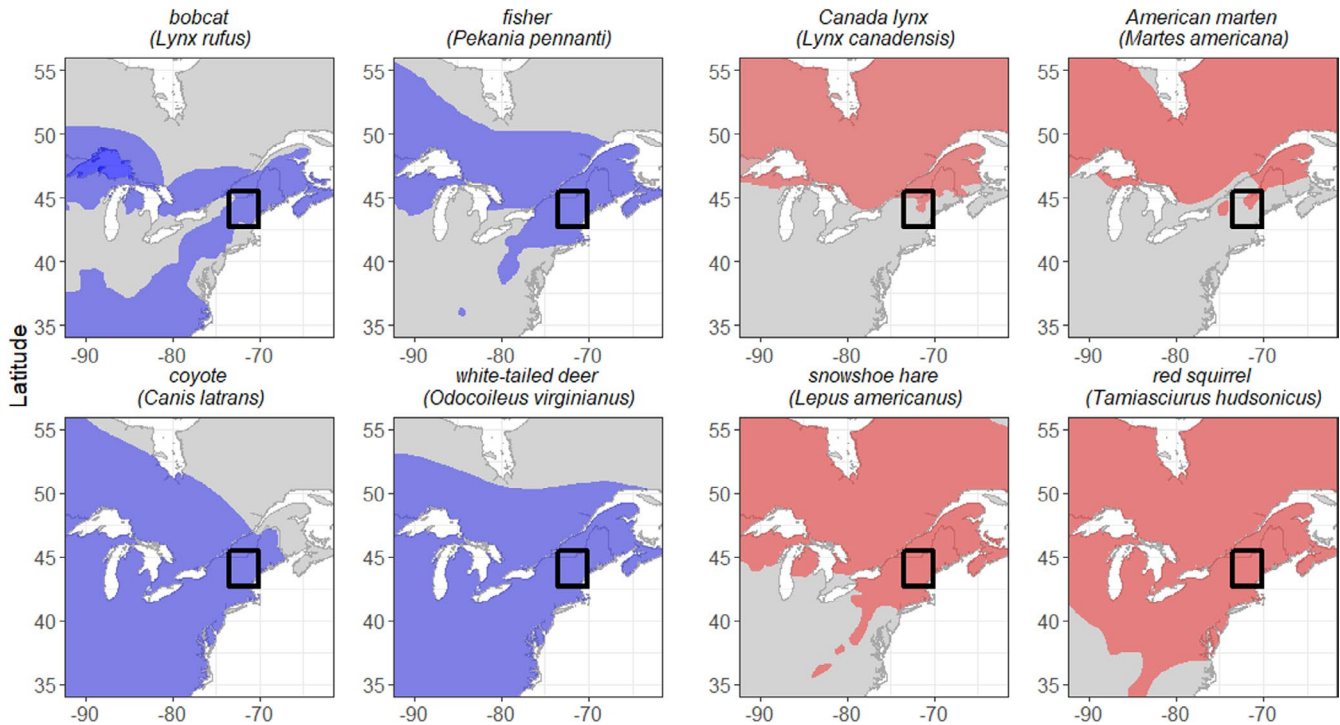
FIGURE 1 Range maps of carnivore and prey species along or near cold (blue) and warm (red) range limits in the region (black box) sampled in this study. Maps were downloaded from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Version 2020–2 http://www.iucnredlist.org) on 10 November 2020. Note: Our sampling included the regional limits or areas of low occupancy of fishers, red squirrels, and deer not captured by IUCN maps. The warm edge of martens was expanded to reflect its contemporary range in our study region (Krohn, 2012). Red fox (data not shown) are considered cosmopolitan in the region and throughout most of North America.

limits (Table 1, Figure 2). Following this idea, we predicted that snow would have a positive and indirect effect and mediate competitive interactions for carnivore populations along warm edges (Table 2, Figure 2).

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area was located in the northeastern United States within the states of New Hampshire and Vermont (Figure 3). This region is part of the transition zone between the northern hardwood and boreal forests, where ecological communities that occur all the way north to Alaska meet those from the southeastern United States (Goldblum & Rigg, 2010). Elevation of our sampling ranged from the lowest valleys at 3 m to the highest peaks in the region at 1487 m and latitude ranged between 42.8 and 45.3°N (Figure 3). 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 and 160 cm and snowfall ranges from 244 to 406 cm, with deeper snow at high elevation and northern regions (Davis et al., 2013). July is the warmest month averaging 18°C

(11°C–27°C) and January the coldest month averaging −11°C (−15°C to −2°C).

2.2 | Data collection

2.2.1 | Camera surveys

We used data from 257 camera-trap sites spaced in non-overlapping grids based on the home range size of the smallest carnivore species (marten = 2 × 2 km; Sirén et al., 2016) (Figure 3). 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 toward a stake positioned 3–5 m from the camera (Figure 3, inset). Commercial skunk lure and turkey feathers were used as attractants and placed directly on the snow stakes. Cameras were set to take 1–3 consecutive pictures every 1–10 sec when triggered, depending on the brand and model, and checked on average 3 (range = 1–9) times each season to download data, refresh attractants, and to ensure cameras were working properly.

2.3 | Statistical methods

We adopted a two-step modeling approach to evaluate our hypotheses. First, we used detection/non-detection data of six carnivore and

TABLE 1 Description of predictor and response variables used in occupancy and structural equation model (SEM) analyses, including the category, variable name, analysis (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	Mean snow depth, Max depth, Snow duration	ψ, 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 for each grid for the study duration (2014–2019).	Snow mediates competition between populations along cold and warm range limits.
Unlinked biotic factor[a]	Biomass	ψ, SEM	McGarigal et al. (2017a)	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.
	Boreal forest, Hardwood forest, Mixedwood forest	ψ	McGarigal et al. (2017b)	Land cover map with forest ecosystem classifications at 30 m resolution in the northeastern USA. https://doi.org/10.7275/R5P8494J	Forest cover types provide habitat for prey and predators, imparting bottom-up effects.
	Prey availability	ψ, SEM	Data from this study	Occurrence data of white-tailed deer, snowshoe hare, and red squirrels detected at camera sites. Occupancy models were fit for each species to generate BUPs for SEMs.	The availability of ecologically important prey species influences the distribution of carnivores.
Biotic interactors	Carnivore occurrence	ψ, SEM	Data from this study	Occurrence data of bobcats, coyotes, fisher, and red fox detected at camera sites. Occupancy models were fit for each species to generate BUPs for SEMs.	The distribution of competing carnivores influences the distribution of focal species (martens and lynx).
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 to 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 a species.
	Time since camera check	ρ	Data from this study	Number of weeks since a camera was checked.	Detection would be highly 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.

[a]Factors that are density independent, not appreciably consumed or contested, and have greater influence at broad spatial scales (Anderson, 2017).
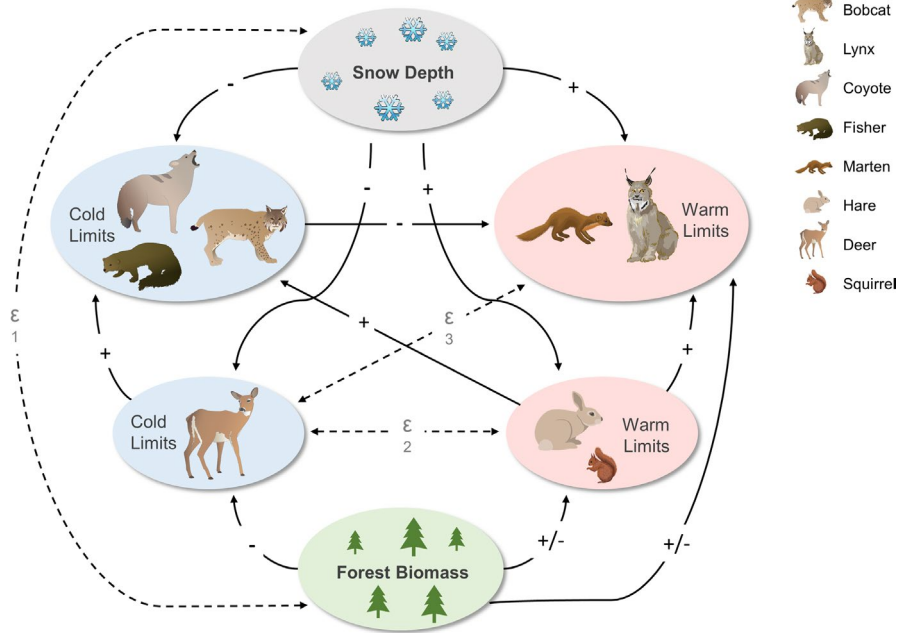
FIGURE 2 Our *a priori* model illustrating the hypothesized effects of snow depth (abiotic), prey and habitat availability (unlinked biotic factors), and biotic interactions (competition) on carnivores along cold and warm range limits in the northeastern United States. Black arrows represent predicted direct effects and unidirectional consecutive arrows pointed in the same direction represent indirect effects. Indirect effects are calculated by taking the product of consecutive path coefficients. For example, the product of the two negative path coefficients between snow depth, fisher, and marten equals a positive indirect effect. Total or net effects are the summation of direct and indirect paths. Dashed lines with double-sided arrows represent free covariances ($\varepsilon^{1,2,3}$). The symbols used are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols).

TABLE 2 Range limit position (Cold, Warm) 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 and 16 May from 2014 to 2019 were used to generate best unbiased predictors (i.e., BUPs) from occupancy models as inputs for SEMs. Note, red fox were found throughout the region and considered cosmopolitan (Cos).

| Species	Limit	Predictions	Notable papers
Bobcat (*Lynx rufus*)	Cold	-snow depth, +deer, +hare, +squirrel	Litvaitis and Harrison (1989); Litvaitis et al. (1986); Newbury and Hodges (2018); Reed et al. (2017)
Coyote (*Canis latrans*)	Cold	-snow depth, +deer, +hare	Litvaitis and Harrison (1989); O'Donoghue et al. (1998); Sirén et al. (2017)
Fisher (*Pekania pennanti*)	Cold	-snow depth, +hare, +squirrel	Jensen and Humphries (2019); Kirby et al. (2018); Manlick et al. (2017)
White-tailed deer (*Odocoileus virginianus*)	Cold	-snow depth, -biomass	Dawe and Boutin (2016); Simons-Legaard et al. (2018)
Red fox (*Vulpes vulpes*)*	Cos	-snow depth, -coyote, +hare	Halpin and Bissonette (1988); Harrison et al. (1989); Sirén et al. (2017)
Canada lynx (*Lynx canadensis*)	Warm	+snow depth, -biomass, -bobcat, -coyote, +squirrel, +hare	Bayne et al. (2008); Ivan and Shenk (2016); O'Donoghue et al. (1998); Peers et al. (2013); Scully et al. (2018)
American marten (*Martes americana*)	Warm	+snow depth, +biomass, -fisher, -red fox, +squirrel, +hare	Carlson et al. (2014); Jensen and Humphries (2019); Krohn (2012); McCann et al. (2010); Sirén (2013); Thompson and Colgan (1987)
Snowshoe hare (*Lepus americanus*)	Warm	+snow depth, -biomass	Homyack et al. (2007); Sultaire et al. (2016)
Red squirrel (*Tamiasciurus hudsonicus*)	Warm	+snow depth, +biomass	McDermott et al. (2020)
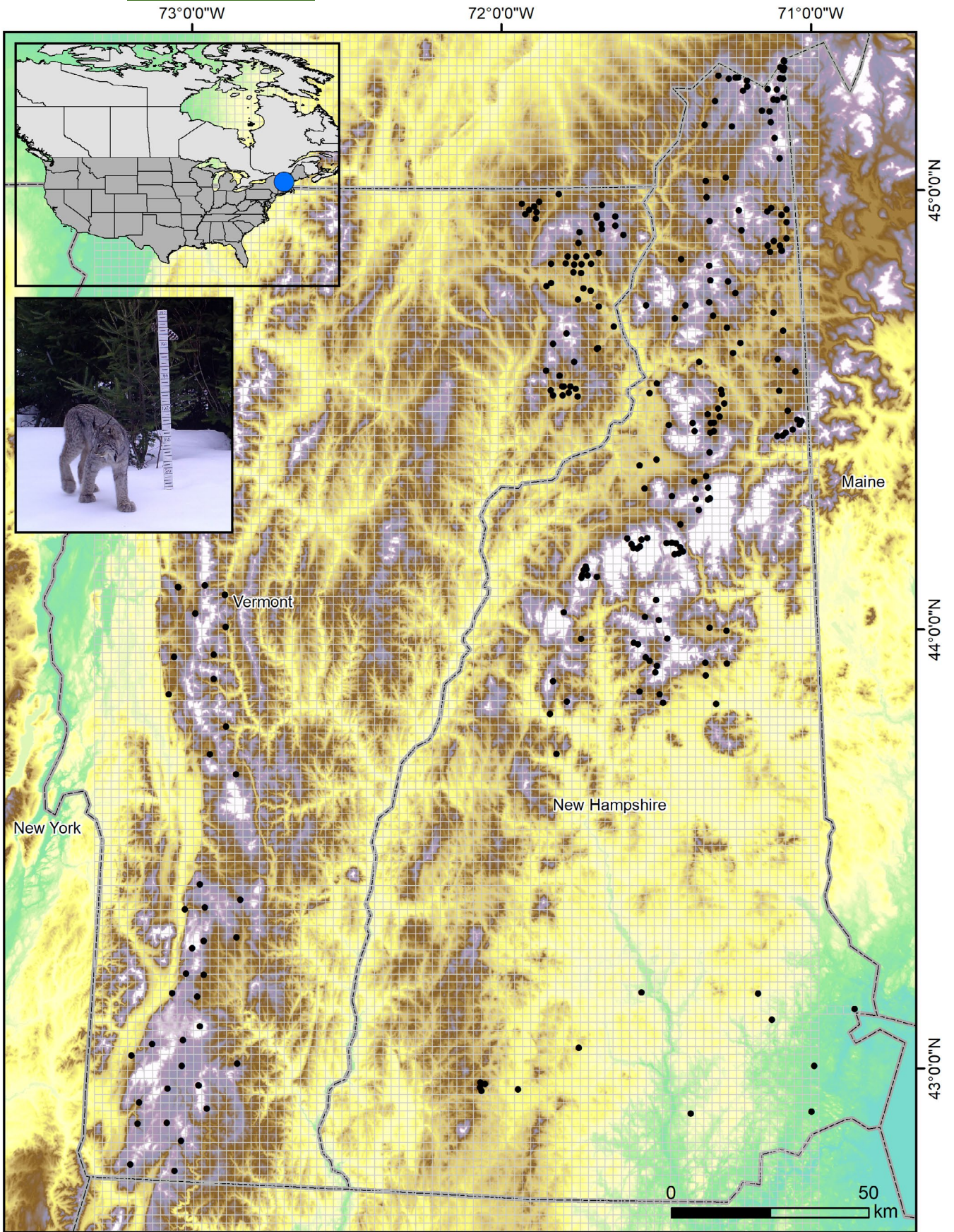
three prey species along or near range limits (see Table 2; Figure 1) from camera surveys to fit single-season occupancy models and derive the best unbiased estimates of occurrence (Kéry & Royle, 2015). We then included these estimates as response and predictor variables within a structural equation modeling (SEM) framework to evaluate hypotheses of iRLT.

2.3.1 | Single-season occupancy models

To generate species occurrence states for the SEM, we used camera data from autumn to spring (16 October–15 May) for each year (2014–2019). This seasonal range was chosen as it approximates demographic (i.e., births and deaths) and geographic closure (i.e., dispersal) and is based on species' ecological responses to snowpack and leaf phenology of the region (Sirén et al., 2016; Vashon et al., 2008). We identified species in photographs by their unique morphology and field marks and used consensus from multiple observers when identification was uncertain (Thornton et al., 2019). 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 modeling framework (MacKenzie et al., 2017).

To generate best unbiased estimates of occurrence (BUPs), we fit a saturated model for each carnivore and prey species, including several covariates on detection and occupancy (Table 1). Because we used data from multiple years, we used a 'stacked' design and specified 'Year' as a fixed effect on detection and occupancy probability. 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 (Table 1). We fit a second-order polynomial for week as we expected a non-linear relationship between detection probability and week for most species. We modeled occupancy probability as a function of several snowpack and forest cover type/biomass variables (Table 1). Prior to modeling, we screened all detection and occupancy covariates for multicollinearity using a variance inflation factor (VIF) test with a conservative cutoff (VIF <2; Zuur et al., 2010). Detection covariates all had VIF scores <2, indicating no multicollinearity, so we allowed all covariates in models. Some occupancy covariates had VIF scores >2, so we eliminated those with the highest scores until we found a set of occupancy covariates that exhibited no multicollinearity (VIF scores <2). In summary, we fit a saturated model on detection and occupancy for each species, accounting for multicollinearity and convergence, to maximally explain occurrence (conditional on the data). All occupancy analyses were performed

in R (R Core Team, 2019) using the 'unmarked' package (Fiske & Chandler, 2011).

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 1000 bootstrapped iterations of the saturated model for each species. We considered models to fit the data if the summed square of residuals (SSE) were within the distribution of the bootstrapped SSE (Kéry & Royle, 2015).

For each species, we extracted the empirical best unbiased predictor of occupancy (i.e., BUPs) from camera survey locations during each year they were operational using the 'ranef' and 'bup' functions in 'unmarked' (Fiske & Chandler, 2011). We then used these corrected estimates of carnivore and prey occurrence (the binary mode of the posterior distributions) as response or biotic predictor variables in the SEM to evaluate direct and indirect drivers of species' occurrence patterns (Table 1, Figure 2).

2.3.2 | Structural equation modeling

Structural equation modeling is generally described as a series of univariate regressions within a causal graph or network of paths that allows for the evaluation of complex and competing hypotheses about direct and indirect casual relationships (Grace, 2008). While the focus of correlative approaches is on single processes or responses and provides measures of associations, SEM disentangles correlated variables to identify causal relationships, making it ideal for evaluating ecological and biogeographical theories (Grace, 2008; Wisz et al., 2013), including the direct and indirect hypotheses of iRLT. Moreover, pairing SEM with occupancy models allows direct and indirect effects on species' distributions to be evaluated while accounting for the pervasive issue of imperfect detection (Joseph et al., 2016). For a detailed overview of SEM, including the approach we used for evaluating iRLT (piecewise SEM), and how it differs from correlative statistics, see Text S1 in Supporting Information.

We specified snow depth (cm) and forest biomass (metric tons/ha) as exogenous variables in the SEM (Table 1, Figure 2), using SNODAS (Barrett, 2003) and forest succession and disturbance (McGarigal et al., 2017) data, respectively. Forests with lower biomass values were considered early-successional forest, whereas those with higher values were late-successional (McGarigal et al., 2017). We smoothed the snow depth and biomass layers using a Gaussian kernel function in the 'gridkernel' package (Plunkett, 2019) with a custom bandwidth that was relevant to the scale of our sampling (4 km² grids) and extracted smoothed values from

the camera survey locations using the 'extract' function in the 'raster' package (Hijmans et al., 2015). Our sampling focused more on forested areas with deeper snow depth compared to the broader region (Figure S1).

Using snow depth and forest biomass as exogenous variables and derived estimates of carnivore and prey occupancy (i.e., BUPs) as response and predictor variables, we employed conditional separation or d-sep tests (Lefcheck, 2016) to identify direct and indirect effects. Prior to inclusion in the SEM, we z-score standardized exogenous variables to improve model estimation and compare effect strengths (Grace et al., 2018). We fit a series of univariate generalized linear mixed-effects models (binomial distribution with logit-link function) in the SEM using the 'lme4' package (Bates et al., 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 (Figure 2). We assessed d-sep of the SEM by evaluating the Pearson's chi-squared statistic of a Fisher's C test, where a $p > 0.05$ indicates adequate fit of the observed data and conditional independence (Lefcheck, 2016). If the 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 (Figure 2). Total or net effects were calculated as the summation of direct and indirect paths. 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 indicate the proportion of variance explained by the fixed and random effects. We used the 'piecewiseSEM' package in R (Lefcheck, 2016) for SEM modeling.

3 | RESULTS

3.1 | Camera surveys

From 9 January 2014 to 8 May 2019 (6 winters), we surveyed carnivore and prey species using remote cameras in 257 grids for a total of 15,034 weeks of sampling (**2014**: 62 cameras, 762 weeks; **2015**: 78 cameras, 1,295 weeks; **2016**: 99 cameras, 1,851 weeks; **2017**: 128 cameras, 2,487 weeks; **2018**: 182 cameras, 4,141 weeks; and **2019**: 187 cameras, 4498 weeks). The number of detections and sites occupied varied by species with prey species detected more frequently than carnivores (Table S1). The number of detections (weekly) over the entire study varied by species ($\overline{x} = 784 \pm 243$ SE, range = 69–2500) as did the number of sites occupied ($\overline{x} = 144 \pm 20$ SE, range = 28–198) and naïve occupancy ($\overline{x} = 0.56 \pm 0.08$ SE, range = 0.11–0.77; Table S1).

3.2 | Single-season occupancy models

We fit saturated detection and occupancy sub-models, accounting for multicollinearity and convergence, for carnivore and prey species (Table S2) to generate species-specific occupancy estimates for SEMs. For all species, the summed square of residuals (SSE) of the top models were well within the distribution of the bootstrapped SSEs, with no evidence for a lack of fit (Table S3).

3.3 | Structural equation models

We evaluated a SEM that represented hypotheses of iRLT and alternative hypotheses on range limits using a piecewise approach. The model fit the data well (Fisher's $C = 6.41$, df = 8, $p = 0.60$), indicating d-sep (i.e., conditional separation) and explained 18%–60% of the variation in carnivore occurrence and 11%–45% of the variation in prey occurrence (Figure 4).

3.4 | Direct and indirect causes of cold limits

Snow depth had a direct negative effect on bobcat and coyote occupancy along their cold (upper) limits (Table 3, Figure 4). The effect of snow depth, however, was weak and non-significant for fishers (Table 3). On the other hand, the availability of deer, and to a lesser extent red squirrels, had a strong direct positive effect on fishers (Table 3, Figure S2). These prey species had an equally strong direct effect on bobcats, countering the negative effect of snow depth, whereas deer had a considerably stronger direct effect than snow depth on coyotes (Table 3, Figure 4). Snow depth also had an indirect negative effect on coyotes, bobcats, and fishers due to its negative influence on deer (snow depth → deer → coyote/bobcat/fisher; Table 3, Figure 4). Indirect effects of snow depth were countered, especially for bobcats, by a positive direct effect of snow depth on hares; however, this prey species did not impart strong effects on these carnivores (Table 3). Forest biomass had an indirect effect on bobcat, coyote, and fisher occupancy, specifically through its direct effect on deer (Table 3, Figure 4, Figure S2).

3.5 | Direct and indirect causes of warm limits

Snow depth had a direct and positive influence on lynx and marten occupancy (Table 3, Figure 4). Coyotes had the strongest negative direct effect on these species (Table 3, Figure 4). Bobcats also had a negative direct effect on lynx (Figure 4); however, there was high uncertainty with this relationship (Table 3). The direct negative effect that snow depth had on these competitors produced an indirect positive effect on lynx and martens (snow depth → competitors → lynx/martens; Table 3, Figure 4). Of competing species, bobcats had

FIGURE 4 Structural equation model (SEM) evaluating direct and indirect effects of snow depth, forest biomass (metric tons/ha), and prey availability on coyote, bobcat, and lynx occurrence. All black lines indicate significant path coefficients and conditional R^2 values are provided in rectangles to the upper-left of each species. The symbols used are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols).
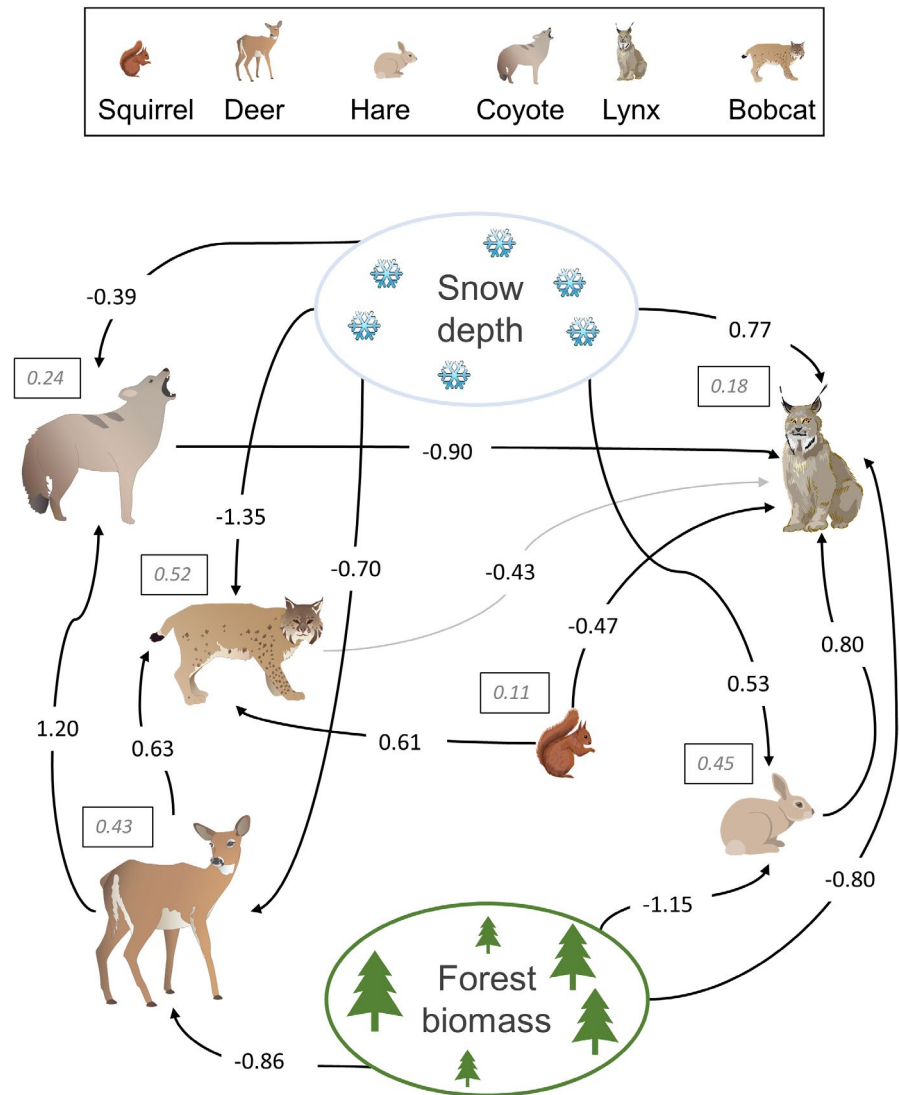
the strongest total net effect on lynx due to a shared, yet opposite, relationship with snow depth (Table 3). Coyotes imparted the strongest total effect for martens (Table 3). Interestingly, squirrels had a marginally significant negative effect on lynx, whereas this prey species imparted a strong positive effect on bobcats and martens (Table 3, Figure 4, Figure S2). Snowshoe hares, on the other hand, had a strong and positive direct effect on lynx and marten occupancy and there were strong indirect effects through snow depth and forest biomass (snow depth/biomass → hares → lynx/marten; Table 3, Figure 4). Forest biomass exhibited a negative direct effect, indicating that lynx were more likely to occur in early-successional forests; the opposite pattern occurred for martens (Table 3, Figure 4, Figure S2).

3.6 | Influence of red fox on community dynamics

Coyotes and fishers had a direct positive effect on red fox occurrence, as did forest biomass (Table 3; Figure S2). Snowshoe

hares, however, had a negative effect on red fox (Table 3, Figure S2). Snow depth did not have any effect on red fox and this species did not impart strong effects on marten occurrence (Table 3).

4 | DISCUSSION

It is typically assumed that biotic interactions limit species along warm range edges, although support for this hypothesis is equivocal (Cahill et al., 2014). Furthermore, few studies have given credence to the potential for positive biotic factors to ameliorate harsh climate along cold-edge limits (but see Prugh & Sivy, 2020). Our study is, to our knowledge, the first to apply a SEM framework to test explicit hypotheses about the direct and indirect effects that determine range limits. As such, we were able to disentangle several correlated abiotic and biotic factors and shed light on previous work. Most importantly, our results illustrate that abiotic stress can mediate competition along warm range limits, supporting iRLT (Sirén & Morelli,

TABLE 3 Path coefficients for structural equation model (SEM) indicating direct (SE), indirect, and total or net effects of snow depth (snow), forest biomass (bio), prey, and competing species on carnivores. Direct path coefficients highlighted in bold were deemed significant.

Direct effects	Bobcat	Coyote	Red fox	Fisher	Hare	Deer	Squirrel	Snow	Bio
Bobcat	-	-	-	-	0.43 (0.33)	0.63 (0.32)†	0.61 (0.29)*	-1.35 (0.25)***	-
Lynx	-0.43 (0.41)	-0.90 (0.27)***	-	-0.22 (0.26)	0.80 (0.33)***	-	-0.47 (0.28)†	0.77 (0.13)***	-0.80 (0.17)***
Coyote	-	-	-	-	0.14 (0.21)	1.20 (0.2)***	0.07 (0.2)	-0.39 (0.12)***	-
Red fox	-0.03 (0.26)	0.92 (0.22)***	-	0.88 (0.22)***	-0.46 (0.22)*	0.09 (0.23)	-	0.13 (0.12)	0.73 (0.13)***
Fisher	-	-	-	-	0.28 (0.24)	0.90 (0.23)***	0.47 (0.22)*	-0.13 (0.14)	-
Marten	-	-0.74 (0.27)**	0.2 (0.29)	0.07 (0.28)	0.96 (0.29)***	-	0.65 (0.26)*	1.98 (0.22)***	1.01 (0.2)***
Hare	-	-	-	-	-	-	-	0.53 (0.16)***	-1.15 (0.17)***
Deer	-	-	-	-	-	-	-	-0.70 (0.15)***	-0.86 (0.17)***
Squirrel	-	-	-	-	-	-	-	-0.11 (0.10)	-0.06 (0.1)

Indirect effects	snow → bobcat	snow → coyote	snow → fisher	snow → hare	snow → deer	snow → squirrel	bio → hare	bio → deer	bio → squirrel
Bobcat	-	-	-	0.23	-0.44	-0.07	-0.50	-0.54	-0.03
Lynx	0.58	0.35	0.03	0.43	-	0.05	-0.92	-	0.03
Coyote	-	-	-	0.08	-0.84	-0.01	-0.17	-1.03	0.00
Red fox	0.04	-0.36	-0.12	-0.24	-0.07	-	0.53	-0.08	-
Fisher	-	-	-	0.15	-0.63	-0.05	-0.32	-0.77	-0.03
Marten	-	0.29	-0.01	0.51	-	-0.07	-1.10	-	-0.04

Total (net) effects	snow + snow → bobcat	snow + snow → coyote	snow + snow → fisher	snow + snow → hare	snow + snow → deer	snow + snow → squirrel	bio + bio → hare	bio + bio → deer	bio + bio → squirrel
Bobcat	-	-	-	-1.12	-1.79	-1.41	-	-	-
Lynx	1.36	1.13	0.80	1.20	-	0.82	-1.72	-	-0.78
Coyote	-	-	-	-0.32	-1.24	-0.40	-	-	-
Red fox	0.17	-0.24	0.01	-0.12	0.06	-	1.25	0.65	-
Fisher	-	-	-	0.02	-0.76	-0.18	-	-	-
Marten	-	2.27	1.97	2.49	-	-	-0.09	-	0.97

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, †$p < 0.1$.

2020) and providing critical understanding of how a warming climate may alter species interactions and distributions (Urban et al., 2016; Wisz et al., 2013).

We found support for our hypothesis that snow directly limits populations along cold 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 and coyotes. Prior studies have found these species to have a negative association with deep snow (Dowd et al., 2014; Reed et al., 2017), likely due to limited mobility that can contribute to starvation (Bekoff & Wells, 1981; Litvaitis et al., 1986). Snow had a negative effect on fishers, but this effect was weak in contrast with other studies (e.g., Zielinski et al., 2017). However, the availability of primary prey species, which were generally higher in low biomass forests, countered the negative effect of snow for these carnivores, indicating the importance of food in areas with adverse climate. Indeed, the reliance on a diversity of prey, and larger prey species in particular, is important for northern bobcat and coyote populations during winter (Litvaitis et al., 1986; Litvaitis & Harrison, 1989; Newbury & Hodges, 2018). Similar results have been found for fishers living in deep snow regions (Jensen & Humphries, 2019; McLellan et al., 2018), supporting our findings. However, harsh winters may only benefit certain segments of a population (e.g., adult males, Litvaitis et al., 1986). More generally, our results provide insight on how warmer winters and an abundant prey base that includes temperate and boreal species may fuel range expansion for carnivore populations along cold limits (Sirén & Morelli, 2020).

Our study highlights the negative effect that competitors have on populations along warm limits, consistent with the long-standing hypothesis that biotic interactions are more influential along warm range boundaries (Louthan et al., 2015). Moreover, our results also indicate strong support for iRLT. For example, snow had a strong positive effect on lynx and marten occupancy along their warm limits. These results are consistent with other studies (Hostetter et al., 2020; Hoving et al., 2005; Jensen & Humphries, 2019; Ray et al., 2018). However, there was also evidence of an indirect effect for lynx; snow depth-mediated occupancy of coyotes and bobcats, its primary competitors that had a negative effect on lynx occupancy. Moreover, there was a positive, indirect effect of snow on martens through a direct negative effect of snow on coyotes. This was less prominent than the coyote/bobcat–lynx relationship but is aligned with our hypothesis of how climate mediates competition along warm limits and also potentially explains the positive association with snow commonly identified by other studies (see review in Sirén & Morelli, 2020).

We were surprised by the strong negative effect that coyotes had on martens. Although martens are known to be preyed upon by coyotes, more common predators include fishers and red fox (McCann et al., 2010; Sirén, 2013). 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; 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). Indeed, we found that this species had a strong impact on other species. For example, several carnivores had a shared positive relationship with deer that may indicate carrion provisioning by this top carnivore (Jensen & Humphries, 2019; Prugh & Sivy, 2020; Sivy et al., 2017). Coyotes, and also bobcats, kill deer in northern regions (Litvaitis & Harrison, 1989; Major & Sherburne, 1987), potentially providing scavenging opportunities for fishers and red fox, and explaining the positive associations these carnivores had with deer. However, positive associations do not mean that competitive interactions are absent at other scales (Prugh & Sivy, 2020; Sivy et al., 2017). For instance, coyotes have been shown to be a dominant competitor of red fox at local scales (Major & Sherburne, 1987). In addition, although the occupancy–abundance relationship for territorial carnivores is strong (e.g., Linden et al., 2017), the coarse-scale resolution of occupancy data might preclude a nuanced understanding of competitive interactions between species. Clearly, more community-level demographic studies are needed to differentiate the true competitors from the indirect ones. Future research could compare competitive dynamics using occupancy versus abundance and include dietary analyses to better assess niche dynamics and the role of coyotes on the ecological community.

From a lynx conservation perspective, we found that a combination of competitors limit this federally threatened species along its southern range boundary. In particular, coyotes, bobcats, and, recently, fisher are considered the primary threat to lynx populations in the conterminous United States (Bayne et al., 2008; McLellan et al., 2018; Peers et al., 2013). The negative effect of coyotes on lynx was evident but less certain for bobcats. However, we found bobcats to have the greatest potential impact on lynx occupancy through the indirect effect of snow and associations with similar prey. Bobcats and lynx are phylogenetically similar (Koen et al., 2014) and can have similar diets (Ivan & Shenk, 2016; Litvaitis et al., 1986; Newbury & Hodges, 2018); thus, competition between these species should be fierce and result in exclusion at broad spatial scales (Godsoe et al., 2017). Indeed, these species rarely co-occurred during our study, whereas coyotes and fishers overlapped considerably with lynx. Furthermore, the opposite effect that red squirrels had on lynx (negative) and bobcats (positive) may suggest that bobcats (and potentially fishers and martens) are preventing lynx from accessing this important secondary prey species. Because snowpack is expected to decline in the northeastern United States and elsewhere along the southern limit of lynx range (Diro & Sushama, 2020), the concern is that bobcat will outcompete lynx and contribute to ongoing range contraction along its warm limit (Peers et al., 2013). Our study provides convincing evidence for this possibility and suggests that natural resource managers may need to consider innovative solutions to alleviate these biotic constraints or accept the change in distributions. We see several potential management actions, including: (a) protecting climate change refugia through land conservation planning (Morelli et al., 2016), (b) managing forests to increase snowpack retention and promote boreal forest (Dickerson-Lange et al., 2017),

and (c) directly controlling competitors (e.g., predator management). Although challenging, these decisions are timely considering that lynx were recently recommended for delisting (US Fish & Wildlife Service, 2017).

By using SEM, we were able to show that abiotic factors and biotic interactions can be intercorrelated. The effect of these intercorrelations has been demonstrated through simulation (Godsoe et al., 2017) and cited as a reason why many past studies might have failed to detect the role of biotic interactions along warm range limits (Sexton et al., 2009; Sirén & Morelli, 2020). This issue was resolved using SEM, which allows for the inclusion of correlated predictors to identify direct and indirect effects on a response (Grace, 2008). Besides using SEM, we also collected large-scale data on biotic interactors (i.e., competitors and prey) and sampled beyond the range limit of several species. Both of these approaches have been advocated by previous work (Wisz et al., 2013) to understand causes of range limits. As such, we were able to show that abiotic stress mediates competition along warm range limits and that positive biotic factors can ameliorate harsh climate along cold limits. Ideally, though, experimental work coupled with demographic studies will confirm these dynamics.

Our modeling approach has some caveats worth noting. We adopted a two-stage approach in which we generated estimates of the occupancy states that we then used in the SEM. Although this is the standard approach (e.g., Mills et al., 2020; Sivy et al., 2017), it does not incorporate uncertainty of the occupancy state in the SEM, and hence the errors do not propagate. We partially remedied this by modeling occupancy using a saturated model to maximally explain spatial variation in occupancy. An alternative approach, developed by Joseph et al., (2016), jointly integrates occupancy modeling and SEM. However, it is unclear how to perform this integration using piecewise SEMs, the approach we used in this study. As SEM approaches become increasingly adopted to analyze observational data using hierarchical models, we suggest further methodological development and guidance of integrated SEMs (*sensu* Joseph et al., 2016) and encourage users to understand the implications for modeling choices in the generation of estimates of the underlying state.

Because biotic interactions are important along warm 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 models 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 et al., 2016) and potentially allow for population persistence in some regions. 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 suggest using theoretical and analytical frameworks such as iRLT and SEM, respectively, to disentangle these factors. Once direct and indirect effects are known, they can be used as a heuristic tool for understanding which actions can be used to conserve threatened species and manage those expected to win out.

DATA AVAILABILITY STATEMENT
Data included in the manuscript is publicly available in Dryad (https://doi.org/10.5061/dryad.q2bvq83j5).

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BIOSKETCH

Alexej Sirén is an ecologist studying the effects of climate and land use change on wildlife populations and communities of North America. The goal of his work is to advance ecological theory, develop practical to tools for monitoring climate and wildlife, and provide natural resource agencies robust data for making conservation and management decisions. The coauthors of this study are a diverse team of scientists that focus on quantitative ecology, climate change adaptation, and wildlife and forest management.

Authors' contributions: APKS designed the study. APKS, CAB, KJR, JRK, CC, RMC, & LSP collected and contributed data. APKS & CAB curated the data. APKS conducted the analysis and wrote the first draft of the manuscript with edits from CSS and TLM. All authors made substantial edits and approved the final manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.