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Research article

Does habitat or climate change drive species range shifts?

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A primary prediction of climate change ecology is that species will track their climate niche poleward and upslope. However, studies have shown species responding in surprising ways. In this study, we aim to understand the impact of global change on species ranges by considering both climate and habitat changes. Using occupancy analysis of acoustic survey data in the mountains of the northeastern United States, we tested specific predictions of range responses to warming (shifting upslope), precipitation change (shifting downslope), and forest composition change (shifting downslope). We found that American red squirrels *Tamiasciurus hudsonicus*, key nodes in northern North American food webs, are not tracking increasing temperatures upslope, despite substantial warming in recent decades. Structural equation modeling indicates that red squirrel abundance is primarily influenced by red-spruce forest cover, which has shifted downslope with recovery from historical logging and acid deposition. Accounting for the multiple dimensions of global change will enable better predictions and more effective conservation strategies.

Keywords: climate change, indirect effect, lag effect, land use change, montane, range shift

[Correction added after first online publication on 28 February 2025, First author name was corrected in How to Cite.]

Introduction

As anthropogenic climate change increasingly impacts every ecosystem across the globe, terrestrial wildlife populations are generally expected to track temperatures poleward

and upslope (Lenoir and Svenning 2015, Lawlor et al. 2024). Although there is evidence of these predicted responses (Parmesan and Yohe 2003, Weiskopf et al. 2020), exceptions exist where species' ranges are either not moving or are shifting in the opposite direction (Tingley et al. 2012, Rapacciuolo et al. 2014, Rowe et al. 2015, Alexander et al. 2018, Rubenstein et al. 2023). Such unexpected patterns highlight the need for better predictions of how and when species will respond spatially to climate change. Better spatial predictions can inform decisions regarding fundamental conservation actions such as conservation easements, land acquisitions, reintroductions, and invasive species and habitat management. Without such information, conservation will be much less effective (Urban et al. 2016, Morelli et al. 2020). Given limited budgets for conservation and the ongoing biodiversity crisis, as highlighted in reports of drastic losses in abundance of birds and insects (Lister and Garcia 2018, Rosenberg et al. 2019, Sánchez-Bayo and Wyckhuys 2019, Luedtke et al. 2023), effective conservation is critical.

Better understanding of what determines species range limits will improve spatial predictions. One of the classic questions of ecology is whether species ranges are more strongly determined by abiotic (e.g. temperature, precipitation) or biotic (e.g. habitat, competition) factors (Grinnell 1917, Chase and Leibold 2003, Sirén and Morelli 2020). The relative importance of these niche components is expected to impact a species' response to environmental change (Rowe et al. 2015, Poniatowski et al. 2020, Rossi et al. 2023, Chardon et al. 2024). The urgency of conducting conservation and management in the face of climate change makes this question even more relevant. In addition to differing spatially (e.g. due to climate change refugia, Morelli et al. 2020), the impacts of climate change are likely to differ temporally. There is usually a discrepancy between the rate of change in the direct effects (e.g. extreme heat on thermoregulation) and indirect effects (e.g. temperature and precipitation change on habitat) of climate change, known as a lag effect (Bertrand et al. 2011, Alexander et al. 2018). Yet the indirect drivers of range shifts have rarely been examined to understand and predict the impacts of climate change, although this literature is growing (Duclos et al. 2019, Sirén et al. 2022, Rossi et al. 2023).

Here we use a long-term dataset focused on the American red squirrel *Tamiasciurus hudsonicus* (hereafter red squirrel) to investigate whether climate change is more likely to drive red squirrel range shifts directly via climate or indirectly via habitat changes. Red squirrels inhabit boreal and sub-boreal forests in North America, stretching from Alaska through Canada to parts of western North America, the upper Midwest, the northeastern United States (hereafter Northeast), and south along the Appalachian Mountains at higher elevations into Georgia (Patterson et al. 2007). Red squirrels disperse seeds (primarily from conifers but also deciduous trees in some areas) and fungi. They are also predators of birds (primarily eggs and nestlings; FitzGerald et al. 2019) and are themselves the prey of raptors and mammals, such as the American marten *Martes americana* (Cumberland et al. 2001, Slauson and Zielinski 2017), and so have profound top–down and bottom–up ecosystem impacts. Temperature and precipitation impacts have not been widely studied in red squirrels, although higher spring temperatures seem to increase reproductive success (Réale et al. 2003, Descamps et al. 2008) and juvenile overwinter survival is generally low for American red squirrels (average of 26% surviving their first winter; Rusch and Reeder 1978, McAdam et al. 2007). On the other hand, a study of the boreal Eurasian red squirrel *Sciurus vulgaris* found that they may be negatively affected by warming winters (Turkia et al. 2018). Hotter summer temperatures could increase energetic demands due to effects on thermoregulation and behavioral adaptation interfering with food caching. More snow could increase energy demands and limit access to food caches. The changing precipitation regimes influence fungus availability – a key forage item for red squirrels.

We focus our study on the Northeast, specifically from upstate New York to Maine, where forests have experienced a complex history of deforestation and a century of regrowth (Thompson et al. 2013), accompanied by increases and then decreases in acidic deposition. A combination of related factors led to the dieback of montane forests, which now appear to be recovering. As a result, the ecotone between high-elevation spruce (*Picea* spp.)–fir *Abies balsamea* forest and mixed hardwoods (a mix of northern hardwoods and conifers, hereafter northern hardwoods or just hardwood) at lower elevations has been shifting downslope between −1.3 and −1.5 m year^{-1} over 19 years in the Northeast (Foster and D'Amato 2015). Recent research (Hallworth et al. 2024) found that red squirrel occupancy rates and abundance are highest around this ecotone in the Northeast. The region has also seen, and is expected to continue experiencing, drastic changes in climate. The Northeast warmed faster than much of the continent over the 20th century (Karmalkar and Horton 2021) and precipitation has been increasing (Janowiak et al. 2018, Staudinger et al. 2024). Both temperature and precipitation, particularly winter precipitation, are forecast to continue increasing in the 21st century, at some of the fastest rates in the world (Karmalkar and Bradley 2017).

We set out to understand the degree to which temperature, precipitation, or forest habitat change influences the occupancy and abundance of red squirrels. Occupancy estimates can provide a coarse view of a population's response to environmental change, whereas abundance estimates often provide a more detailed look at a population's status and habitat relationships (Zuckerberg et al. 2009). We predicted that, if temperature is the principal driver of the red squirrel distribution in the Northeast, then occupancy and abundance will have increased at the upper elevational edge – which tops out in the region at approximately 1450 m a.s.l. (Hallworth et al. 2024) – and decreased at the lower elevational edge of the red squirrel's distribution over the last two decades in response to warming trends; July temperature has increased by 1.2°C over the study period. Conversely, if precipitation is the principal driver of the red squirrel range in the region, then occupancy and abundance will have decreased at the upper edge and increased at the lower edge of the red

squirrel's distribution over the last two decades in response to increasing precipitation; July precipitation has increased by 25.9 mm over the study period. Finally, if habitat primarily determines the red squirrel range, then occupancy and abundance will have increased or stayed the same at the lower edge of the red squirrel's distribution over the last two decades, despite climate change, as the forest ecotone in the region has expanded downslope.

Specifically, we predicted an approximately 220 m shift upslope in elevation across the red squirrel's distribution between 1992 and 2018 if the species is tracking its temperature niche, versus a 41 and 45 m expansion downslope if it is tracking precipitation or habitat, respectively (Fig. 1). We estimated the elevation shift required to maintain occupancy in their realized climate niche from observed temperature changes at our survey sites using a temperature lapse rate of 0.6°C 100 m^{-1} elevation and a precipitation lapse rate of 0.67 mm 100 m^{-1} elevation (Hubbard Brook Experimental Forest, NH). Estimates of change in habitat were derived for 1991–2010 from Foster and D'Amato (2015), who found the spruce-fir montane forest is expanding downslope on average by 1.5 m $year^{-1}$. Our analysis focuses on how accounting for the lag effects of climate change, via delayed responses of habitat, could enable better predictions and ultimately more effective conservation.

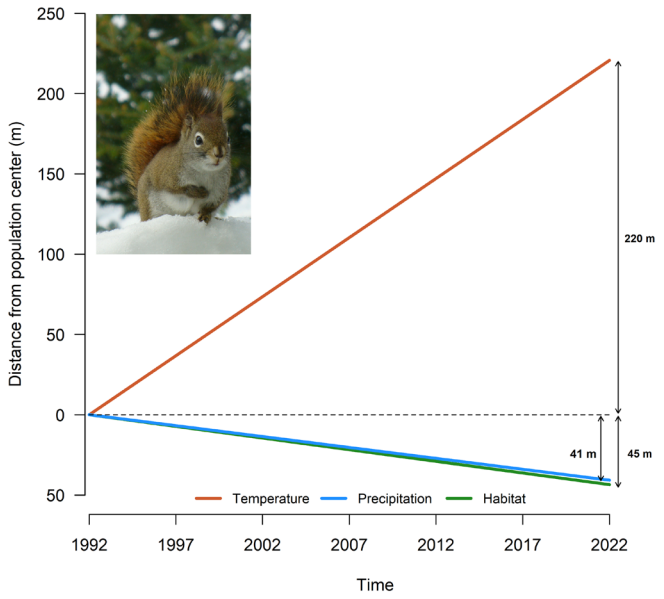

Figure 1. If American red squirrel *Tamiasciurus hudsonicus* populations across the northeastern U.S. track temperature directly and exclusively, their distribution is predicted to have increased upslope by 220 m (red line) since 1992, estimated from observed temperature changes at our survey sites between 1992–2018 using a temperature lapse rate of 0.6°C 100 m^{-1} elevation (Hubbard Brook Experimental Forest). In contrast, we predicted a 41 m (blue line) and 45 m expansion (green line) downslope if they are exclusively tracking increased precipitation or habitat change, respectively. Estimates of change in habitat were derived from Foster and D'Amato (2015) who found the spruce–fir montane forest is expanding downslope at approximately 1.5 m $year^{-1}$. Image by S. Faccio.

Material and methods

Occupancy modeling

We capitalized on a 27-year (1992–2018), regional scale auditory survey dataset (n = 2390 sites, Hallworth et al. 2024, Supporting information) to test for elevational distribution changes through time. The auditory surveys were intended to draw inference about spatial and environmental factors affecting red squirrel abundance. For both the surveys used in the occupancy and abundance modeling, standard procedures established across the literature were implemented to ensure that model assumptions were not violated (e.g. closure, Chandler et al. 2011). We used standard point count protocol for our surveys (Kery and Royle 2015) involving a 10-min survey period divided into 4 × 2.5 min intervals during which individual red squirrels (and birds) were recorded according to two distance categories – within and beyond 50 m where we assumed closure (i.e. individuals were not varying in their movements, but only detectability, Duclos et al. 2019). Field technicians only counted more than one individual if they heard them calling at the same time or if they saw two separate individuals. Survey locations were spaced > 250 m apart across the Northeast landscape, which varies from northern hardwood to montane spruce–fir forest.

We used a dynamic occupancy modeling framework to derive yearly red squirrel occupancy estimates along a > 1000 m elevational gradient in the northern Appalachian Mountain region. We included parameters in the occupancy model known to influence occupancy of red squirrels. Those include distance from the center of the transition zone between the northern hardwood and montane spruce-fir forest (ecotone), and the probability of American beech and balsam fir mast (Hallworth et al. 2024). We modeled initial red squirrel occupancy ($Z_{[i,1]}$) at each survey location (i) following

$$Z_{i,1} \sim \text{Bernoulli}\left(\psi_{i,1}\right)$$

$$\text{logit}\left(\psi_{i,1}\right) = \alpha_i + \beta 1 \times \text{Ecotone}_i + \beta 2 \times \text{AmBeech}_{i,1} + \beta 3 \times \text{BalsamFir}_{i,1} + \ _1$$

Subsequent years (k) were modeled following

$$Z_{i,k} \sim \text{Bernoulli}\left(\mu_{i,k}\right)$$

$$\text{logit}\left(\mu_{i,k}\right) = \alpha 1_i + \Gamma \times Z_{i,k-1} + \beta 1 \times \text{Ecotone}_i + \beta 2 \times \text{AmBeech}_{i,k} + \beta 3 \times \text{BalsamFir}_{i,k} + \ _k$$

Where Ecotone, AmBeech and BalsamFir represent a site's distance from the center of the ecotone, and yearly estimates of the probability of American beech and balsam fir mast, respectively (Hallworth et al. 2024).

Repeated surveys (r) at each survey location (i) within each year (t) accounted for imperfect detection in our occupancy model. Therefore, we modeled detection probability following

$$y_{i,r,t} \sim \text{Bernoulli}\left(Z_{i,t} \times p_{i,r,t}\right)$$

$$\text{logit}\left(p_{i,r,t}\right) = a_{\text{survey project}} + \beta \times \text{date}_{i,r,t} + \text{eps}_t$$

where y is a binary detection (1 = detected, 0 = not detected) matrix for survey location, Z is the true occupancy latent state, p is detection probability, a is the intercept allowed to vary by survey project, and β is the effect of date on detection. We allowed detection probability to vary by survey date (date) and included an error term (eps) indexed by year (t) to account for unmodeled interannual variation.

To test whether the red squirrel distribution has shifted through time, we derived the elevation of study sites corresponding to occupancy probabilities at 5, 25, 50, 75 and 95% for each year of study. These metrics have been used in this system to describe elevational changes through time (DeLuca and King 2017, Van Tatenhove et al. 2019). We generated expected occupancy estimates using the mean probability of American beech and balsam fir mast each year because mast has been shown to influence the elevational distribution of red squirrels (Hallworth et al. 2024). We fit a linear regression to test for a trend in several occupancy probabilities representing different ecological scenarios (Maggini et al. 2011, DeLuca and King 2017, Van Tatenhove et al. 2019). For example, if the higher edge of the red squirrel distribution is moving upslope, we expect to see a change in the elevation associated with the 95% occupancy probability.

Abundance modeling

We used the same regional scale auditory survey dataset (n years = 27, 1992–2018, n sites = 2390 sites) to estimate abundance to test for elevational distribution changes through time. We derived abundance estimates while accounting for imperfect detection using an open-population N-mixture model (Dail and Madsen 2011). We modeled red squirrel abundance (N) following:

$$N_{i,1} \sim \text{Poisson}\left(\lambda_{i,1}\right)$$

$$\log\left(\lambda_{i,1}\right) = \alpha + \beta_1 x_i \times \beta_2 \text{Mast}_{\text{Beech}_i} + \beta_3 \text{Mast}_{\text{Fir}_i}$$

The abundance at site i in subsequent years k was modeled as

$$N_{i,k+1} \sim \text{Poisson}\left(\rho_{i,k}\right)$$

$$\rho_{i,k} = S_{i,k} + G_{i,k}$$

$$\Phi \sim \text{Uniform}\left(0,1\right)$$

$$S_{i,k} \sim \text{Binomial}\left(N_{i,k}, \Phi\right)$$

$$G_{i,k} \sim \text{Poisson}\left(\Gamma_{i,k}\right)$$

$$\log\left(\Gamma_{i,k}\right) = \gamma_1 + \gamma_2 N_{i,k-1} + \beta_1 x_i \times \beta_2 \text{Mast}_{\text{Beech}_{i,k}} + \beta_3 \text{Mast}_{\text{Fir}_{i,k}}$$

where α and γ represent the intercept in the first and subsequent years. S is the number of surviving individuals at site i in year k which is a function of annual survival (ϕ) and the previous year's abundance. G represents the number of new individuals at a survey location. β_1, β_2, β_3 are slope coefficients for distance from ecotone (x), beech and fir mast, respectively. We accounted for imperfect detection using the same model described above in the occupancy modeling section.

We used the posterior distribution of red squirrel abundance estimates to derive the elevational center of the red squirrel population within our study area for each year of study. We also used the abundance-weighted survey location coordinates to test for a directional change in the center of the population through time. The abundance-weighted coordinates were used to estimate directional change because the occupancy metrics are more sensitive to occupied sites at the periphery of their distribution.

All models were fit using JAGS ver. 3.4.0 (Plummer 2017) in parallel on three chains, each with 100 000 iterations following an initial burn-in phase of 25 000 iterations. We drew every 50th iteration from the posterior distribution to reduce auto-correlation. We accessed JAGS through the 'jagsUI' package in program R ver. 3.6.1 (www.r-project.org). All analyses were conducted on the High-Performance Computing Cluster at the University of Massachusetts Amherst. The posterior mean and 95% credible intervals are reported unless otherwise noted.

Structural equation modeling

We used a structural equation modeling (SEM) framework (Shipley 2016) to evaluate the degree to which squirrel abundance directly correlates with spatial variation in temperature and precipitation as well as indirectly via forest conditions, in effect providing a first-order evaluation of the degree to which this species may be influenced by these abiotic and biotic conditions across its elevational distribution. We used a subset of the sites (n = 150) from a 27-year dataset that also provided fine-scale habitat data (Duclos et al. 2019).

We evaluated the direct and indirect effects of temperature and precipitation on red squirrel abundance in our SEM. We used ClimateNA (Wang et al. 2016) to extract annual predictions of minimum winter (DJF) temperature (°C) and precipitation as snow (cm) at 250 m resolution from each site for the winters of 2013–2014 and 2014–2015. We

chose this approach as site-level temperature and precipitation data were not available and winter conditions seem to influence red squirrel abundance (Rusch and Reeder 1978, McAdam et al. 2007).

We used principal component analysis (PCA) to describe gradients of forest structure and composition from a set of 12 forest variables recorded at each survey location (see Duclos et al. 2019 for details). We interpreted the biological meaning of the first two principal components using factor loadings of < -0.3 and > 0.3 (McGarigal et al. 2013). The two PCA gradients were then used in the SEM as our metrics for vegetation structure and composition. Habitat was represented by a PCA using forest inventory data collected at audio survey locations; the eigenvalues for the first two principal components explained 41% of the variation in the vegetation data. The first principal component (PC1; fir–northern hardwoods gradient; negative to positive eigenvalues) represented a gradient of high-elevation forest comprised of pole-sized (10–22 cm diameter at breast height (DBH) for softwood and 10–30 cm DBH for hardwood) stock characterized by balsam fir *Abies balsamea* and paper birch *Betula papyrifera* trees to a lower elevation hardwood forest comprised of regenerating and saw-sized (> 22 cm DBH (for softwood) and 31 cm DBH (for hardwood)) characterized by red spruce *Picea rubens*, yellow birch *Betula alleghaniensis*, and larger-diameter deciduous trees. The second principal component (PC2; spruce–northern hardwoods gradient; negative to positive eigenvalues) described a forest gradient extending from mixed-woods forest comprised of regenerating and saw-sized DBH stock principally characterized by red spruce to, at the other (positive values) end of the gradient, lower elevation northern hardwoods principally characterized by American beech *Fagus grandifolia* and sugar maple *Acer saccharum* (Supporting information). For a more detailed explanation of the forest structure and composition measurements and PCA see Duclos et al. 2019.

The posterior distribution of red squirrel abundance estimates in our SEM identified the direct and indirect effects of climate and vegetation on red squirrel abundance. We used a multi-group form of SEM to evaluate the direct and indirect effects of climate and habitat on red squirrel abundance (Duclos et al. 2019). Prior to the SEM analysis, we z-score standardized all predictor variables using the scale function in R. We specified correlated errors between temperature and precipitation to account for collinearity between these variables (Shipley 2016) and used the Satorra–Bentler maximum likelihood estimation method as it is robust to deviations from multivariate normality (Satorra and Bentler 1994). In the SEM, direct effects are relationships between two nodes and indirect effects are relationships between nodes that contain an intermediary node and the size and direction of effects are represented through path coefficients (Shipley 2016). We evaluated the goodness of fit of the SEM using several common approaches: χ^2 tests with non-significant probabilities ($p > 0.05$), comparative fit index (CFI) and Tucker–Lewis index (TLI) with values > 0.95, and root mean square error of approximation (RMSEA) with values < 0.07 all indicate a good fit (Hooper et al. 2008). We evaluated the significance of direct and indirect effects using a higher α ($p \leq 0.1$) to mitigate risk of type II errors that stem from known sensitivities of the SEM framework (Shipley 2016, Duclos et al. 2019). We fit the SEM using the 'lavaan' package in R ver. 3.2.2 (Rosseel 2012).

We used an ANOVA test of invariance to evaluate if there were differences between years (i.e. a year effect) and if the addition of 50 new sites during 2015 influenced the path coefficients (i.e. a site effect). For this test, $p > 0.05$ indicates the differences (i.e. effects) between years and sites are negligible and that inference can be made using the multi-group path coefficients (Shipley 2016). Finally, we evaluated the relative importance of direct and indirect effects by comparing absolute values of significant path coefficients comprising direct and indirect pathways (Duclos et al. 2019).

Results

Change in red squirrel occupancy

Between 1992 and 2018, the probability a site was occupied by a red squirrel was 0.44 (95% credible interval (CI) = 0.32–0.56) with yearly estimates ranging from 0.034 (CI = 0.004–0.18) in 2015 to 0.92 (CI = 0.79–0.99) in 2018 following a large mast event. Site persistence, or the probability that a site remained occupied in year t given it was occupied in year $t-1$, varied from a low of 0.36 (CI = 0.11–0.74) between 2005 and 2006 to a high of 0.99 (CI = 0.80–0.99) between 2008 and 2009. Mean detection probability over the duration of the study was 0.33 (CI = 0.20–0.51).

Red squirrels within our sampling region have shifted their distribution downslope since the early 1990s. All five distributional metrics used in our analysis indicate the distribution of red squirrels expanded downslope between 23 and 27 m over the 27-year study period (Table 1, Fig. 2).

Change in red squirrel abundance

The median number of squirrels per site was 1.09 (CI = 0.04–6.34) during the nearly 30-year time-series. Abundance estimates were similar for sites located above (n = 875), within (n = 197), and below (n = 1809) the forest ecotone with an estimated 1.66 (CI = 0.1–4.04), 1.81 (CI = 0.30–4.35), and 2.02 (CI = 0.97–3.80) red squirrels per site, respectively. Similarly, red squirrel population growth estimates did not differ among survey sites above (1.37, CI = 0.50–2.76), within (1.16, CI = 0.59–2.77), and below (0.97, CI = 0.60–2.18) the ecotone; they indicate that the red squirrel population is likely increasing throughout the region.

We used modeled abundance estimates to evaluate whether the elevational center of the population changed through time. We found that the center of the red squirrel population decreased by a total of 60.40 m (95% CI: 25.13–100.84 m) from 1995 to 2018, an annual change of −2.17 m year^{-1} (Fig. 3).

Table 1. Estimates for change in elevation through time. The different occupancy probabilities correspond to elevational distribution of American red squirrels *Tamiasciurus hudsonicus* across the northeastern US; for example, 95 and 5% occupancy probability correspond with the higher edge and the lower edge of the distribution, respectively. The median change estimate and upper and lower 95% credible intervals are shown.

Occupancy probability (%)	Change estimate (slope) (m year^{-1})	95% credible interval
95	−23.00	−34.92: −3.17
75	−23.86	−37.09: −4.54
50	−25.86	−40.19: −7.35
25	−26.67	−43.16: −9.43
5	−24.90	−42.90: −8.84

The abundance weighted geographic center of the red squirrel population within our study region shifted south (158.61°C, CI = 37.50–239.05) with a yearly mean distance of 10.37 km (CI = 1.79–30.84 km) from 1992–2018. However, the interannual movement direction and distance varied from northeast to southwest (Fig. 4).

Temperature versus precipitation versus habitat change effects

We used structural equation modeling (SEM) to determine whether temperature, precipitation, or habitat had stronger effects, directly or indirectly, on red squirrel abundance. The multi-group SEM fit the data well for all goodness-of-fit tests (df = 18, $p < 0.05$, CFI > 0.95, TLI > 0.95, RMSEA < 0.07; Hooper et al. 2008) and the ANOVA test indicated

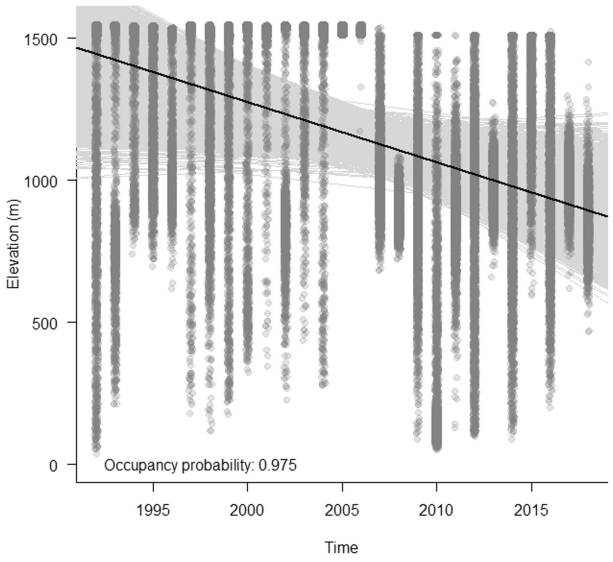

Figure 2. The 95% percentile elevation of sites occupied by American red squirrels *Tamiasciurus hudsonicus* across the northeastern US study area by year. Occupancy estimates were derived using yearly mean estimates of American beech and balsam fir mast. Realizations from the posterior distribution are represented by gray dots with a slight jitter added to show the density of points. The mean trend is shown (black line) along with the uncertainty in trend estimates (light gray lines).

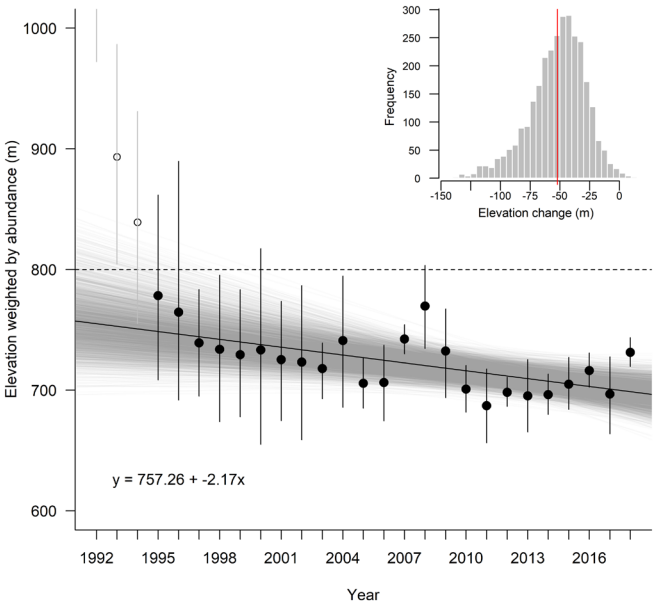

Figure 3. Abundance-weighted mean elevation of American red squirrels *Tamiasciurus hudsonicus* across the northeastern US study area through time. Survey sites remained the same throughout the time series. The black points represent the posterior mean and 95% credible intervals. The mean (solid black line) and trend realizations from the posterior distribution (gray lines) are shown. The dotted horizontal line shows the mean elevation of survey sites without accounting for red squirrel abundance. The open circles are years with small sample sizes that were removed from the analysis. The inset histogram shows the posterior distribution of the overall change in abundance-weighted elevation (m) of the population over the time-series.

no differences between years ($p \geq 0.05$). As such, we interpreted the constrained SEM model results from the full dataset. Precipitation had a negative direct effect on abundance (−0.24; $p < 0.001$; Fig. 5) and a negative indirect effect through the fir–hardwood gradient on abundance (−0.09; p = 0.03). Precipitation also had a positive indirect effect through the spruce–hardwood gradient on abundance (0.08; p = 0.01; Supporting information). However, the strongest effect (direct or indirect) on abundance was the negative direct effect of the spruce–northern hardwood gradient (−0.37; $p < 0.001$; Fig. 5); red squirrel abundance declined as forests transitioned from abundant red spruce to northern hardwoods. Temperature, on the other hand, had smaller direct and indirect effects on abundance than precipitation; temperature had a direct positive direct effect on abundance (0.13; p = 0.02) and a positive indirect effect through the fir–northern hardwoods gradient on abundance (0.05; p = 0.03; Supporting information).

Discussion

Contrary to basic climate change ecology predictions, red squirrel populations in the Northeast are not shifting their distributions based on temperature changes. Rather, they have

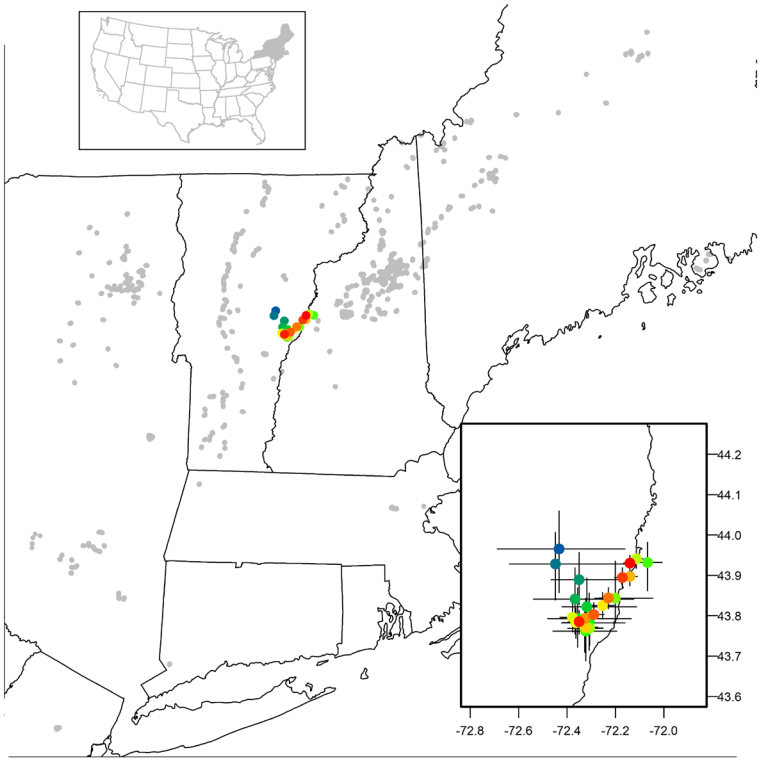

Figure 4. The geographic center of American red squirrels *Tamiasciurus hudsonicus* across the northeastern US study area weighted by their abundance. Survey locations are shown in gray while the colored dots represent the geographic center of the population in each year from 1992 (blue, with smaller sample size) to 2018 (red). The map inset shows a close up of the geographic center along with the 95% credible intervals.

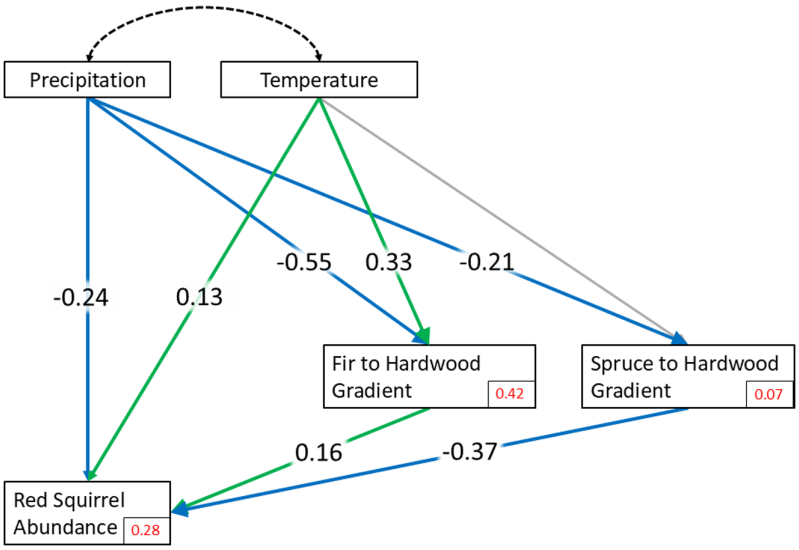

Figure 5. Multi-group structural equation model (SEM) evaluating the direct and indirect effects of temperature, precipitation, and habitat (PC1 = fir–northern hardwoods gradient (ranging from negative to positive eigenvalues); PC2 = spruce–northern hardwoods gradient (ranging from negative to positive PCA eigenvalues)) on American red squirrel *Tamiasciurus hudsonicus* abundance. Direct effects within the SEM are those that contain no intermediary nodes on red squirrel abundance (e.g. precipitation → red squirrel abundance; spruce forest gradient → red squirrel abundance). Positive and negative effects between nodes are indicated by green and blue lines, respectively. The values (red font) in the lower-right corner of the nodes indicate the variance (R2) in response variables explained by the SEM. Double-headed and dashed arrow between precipitation and temperature within the SEM indicates correlated errors and thicker lines indicate significant ($\alpha = 0.1$) relationships.

expanded downslope, a pattern that most strongly correlates with, and thus may be responding to, presence of red spruce forest habitat at lower elevations and increases in precipitation. This result is supported by research that showed spring temperatures did not affect red squirrel distribution dynamics (Van Tatenhove et al. 2019). Our SEM approach confirmed that habitat is likely the mechanistic driver of recent distribution shifts of this spruce forest mammal, although results indicated responses to both direct and indirect effects of climate. Although the precipitation isocline has also shifted downslope, the SEM showed that increased precipitation alone reduced red squirrel abundance. On the other hand, red squirrels slightly benefit from increasing precipitation via the indirect positive effect that precipitation may have on regenerating red spruce. Our SEM results indicate that this forest type had the largest effect (positive), direct or indirect, on red squirrel abundance. There was a smaller effect of fir–hardwood gradient on red squirrel abundance.

The elevational center of the red squirrel population changed at a similar rate as habitat through time (−2.54 m $year^{-1}$ for red squirrels versus −1.5 m $year^{-1}$ for spruce-fir forest). The re-establishment of montane spruce–fir forest along its lower elevation boundary is primarily attributed to recovery from harvesting prior to 1940 and the abatement of acid rain (Foster and D'Amato 2015). Interestingly, the lower elevation (below ecotone) of the red squirrel distribution is also expanding. We have proposed that there is a spillover effect on either side of the ecotone from the positive population effects of the Northeast's roughly biennial tree masting resource pulse that could cause this phenomenon (Hallworth et al. 2024), but more research looking at population demographics and fitness metrics in peripheral regions is needed. Although pulsed food resources (i.e. tree mast) can temporarily ameliorate the upper elevational abiotic constraints for red squirrels (Hallworth et al. 2024), consistent with the interactive range-limit theory (Sirén and Morelli 2020), long-term changes in distributions were more impacted by the gradual re-establishment of montane spruce–fir forest. An alternative hypothesis is that red squirrels were released from biotic interactions (e.g. competition, predation) along their lower distributional elevational edges, supporting theoretical expectations of factors influencing trailing distributional edges (Sirén and Morelli 2020). We did not have data on red squirrel competitors or predators nor are we aware of any major changes in the predator and competitor community in this area during this time frame. However, undoubtedly other factors are also contributing to the population shift, including other climate and non-climate factors that were not modeled, and the interaction among them.

The impact of a red squirrel range expansion could be notable for songbirds of conservation concern in the area. Recent research (Hallworth et al. 2024) showed that increases in red squirrel populations had detrimental effects on songbird populations. If red squirrel populations shift their ranges, there could be cascading effects on the ecosystems that they inhabit.

A primary prediction of climate change ecology is that species will track their climate niche upslope and poleward (Nogués-Bravo et al. 2018, Lawlor et al. 2024). This research is a clear reminder that considering other global change dimensions is crucial. Interestingly, similar shifts (average of 19 m downslope) have been found for high elevation songbirds in the same mountains and for a similar timeframe (DeLuca and King 2017). Given that vegetation changes often lag behind climate changes (Sittaro et al. 2017, Liang et al. 2018), being able to incorporate all of the drivers, direct and indirect, to predict where and when species will shift their ranges will be key to strategizing for effective conservation, including land acquisition and management, in the face of global change (Lawlor et al. 2024). With some exceptions, like breeding songbirds, the red squirrel provides a rare example of an animal for which we have enough data about its habitat, its abundance, and its occupancy over time to begin to understand how global change influences species ranges.

We propose this study as a model for how to improve understanding of how, and when, species will respond to climate change, and why many other species are not responding as predicted to climate change (DeLuca and King 2017, Zimova et al. 2020). Our findings suggest that, as forest composition shifts as a result of global change, the red squirrel distribution will shift in accordance with its preferred habitat. Thus, our study highlights the potential for lag effects on climate-change-induced species range shifts, especially if climate and habitat (or other biophysical drivers) have opposing directions, at least in the near term. Indirect effects of climate change via habitat or species interactions, which SEM can help reveal (Sirén et al. 2022), are more likely to create lagged responses (Stralberg et al. 2015). The timing of species responses is important to determine which conservation actions are implemented by land managers. Some actions have clear and immediate effects, whereas other actions play out over longer time frames (e.g. conservation easements, land acquisitions). In-depth studies such as these can shed light on appropriate future conservation actions for climate-change-vulnerable species.

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Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Michael T. Hallworth**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead). **Timothy Duclos**: Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Adam Ells**: Investigation (supporting); Writing – review and editing (equal). **Steven Faccio**: Conceptualization (supporting); Data curation (supporting). **Jane R. Foster**: Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Kent P. McFarland**: Conceptualization (supporting); Data curation (supporting). **Keith Nislow**: Conceptualization (equal); Writing – review and editing (equal). **Joel Ralston**: Writing - review and editing (equal). **Mary Ratnaswamy**: Conceptualization (equal). **William V. DeLuca**: Conceptualization (equal); Writing - review and editing (equal); Formal analysis (supporting). **Alexej P. K. Siren**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.qfttdz0q8 (Morelli et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J. and Pellissier, L. 2018. Lags in the response of mountain plant communities to climate change. – Global Change Biol. 24: 563–579.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C. and Gégout, J.-C. 2011. Changes in plant community composition lag behind climate warming in lowland forests. – Nature 479: 517–520.

Chandler, R. B., Royle, J. A. and King, D. I. 2011. Inference about density and temporary emigration in unmarked populations. – Ecology 92: 1429–1435.

Chardon, N. I., McBurnie, L., Goodwin, K. J. A., Pradhan, K., Hille Ris Lambers, J. and Angert, A. L. 2024. Variable species establishment in response to microhabitat indicates different likelihoods of climate-driven range shifts. – Ecography 2024: e07144.

Chase, J. M. and Leibold, M. A. 2003. Ecological niches: linking classical and contemporary approaches. – Univ. Chicago Press.

Cumberland, R., Dempsey, J. and Forbes, G. 2001. Should diet be based on biomass? Importance of larger prey to the American marten. – Wildl. Soc. Bull. 29: 1125.

Dail, D. and Madsen, L. 2011. Models for estimating abundance from repeated counts of an open metapopulation. – Biometrics 67: 577–587. https://doi.org/10.1111/j.1541-0420.2010.01465.x

DeLuca, W. V. and King, D. I. 2017. Montane birds shift downslope despite recent warming in the northern Appalachian Mountains. – J. Ornithol. 158: 493–505.

Descamps, S., Boutin, S., Berteaux, D., McAdam, A. G. and Gaillard, J.-M. 2008. Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. – J. Anim. Ecol. 77: 305–314.

Duclos, T. R., DeLuca, W. V. and King, D. I. 2019. Direct and indirect effects of climate on bird abundance along elevation gradients in the northern Appalachian Mountains. – Divers. Distrib. 25: 1670–1683.

FitzGerald, A. M., Whitaker, D. M., Ralston, J., Kirchman, J. J. and Warkentin, I. G. 2019. Taxonomy and distribution of the imperilled Newfoundland gray-cheeked thrush, *Catharus minimus minimus* TT - Taxonomie et répartition de la Grive à joues grises de Terre-Neuve, *Catharus minimus minimus*, en péril. – Avian Conserv. Ecol. 12: 10.

Foster, J. R. and D'Amato, A. W. 2015. Montane forest ecotones moved downslope in northeastern USA in spite of warming between 1984 and 2011. – Global Change Biol. 21: 4497–4507.

Grinnell, J. 1917. The niche-relationships of the California thrasher. – Auk 34: 427–433.

Hallworth, M. T., Sirén, A. P. K., DeLuca, W. V., Duclos, T. R., McFarland, K. P., Hill, J. M., Rimmer, C. C. and Morelli, T. L. 2024. Boom and bust: the effects of masting on seed predator range dynamics and trophic cascades. – Divers. Distrib. 30: e13861.

Hooper, D., Coughlan, J. and Mullen, M. 2008. Structural equation modelling: guidelines for determining model fit. – Electron. J. Bus. Res. Methods 6: 53–60.

Janowiak, M. K. et al. 2018. New England and New York forest ecosystem vulnerability assessment and synthesis: a report from the New England climate change response framework. – Gen. Tech. Rep. NRS-173, p. 234.

Karmalkar, A. V. and Bradley, R. S. 2017. Consequences of global warming of 1.5°C and 2°C for regional temperature and precipitation changes in the contiguous United States. – PLoS One 12: e0168697.

Karmalkar, A. V. and Horton, R. M. 2021. Drivers of exceptional coastal warming in the northeastern United States. – Nat. Clim. Change 11: 854–860.

Kery, M. and Royle, J. A. 2015. Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. Vol. 1: Prelude and static models. – Academic Press.

Lawlor, J. A. et al. 2024. Mechanisms, detection and impacts of species redistributions under climate change. – Nat. Rev. Earth Environ. 5: 351–368.

Lenoir, J. and Svenning, J.-C. 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. – Ecography 38: 15–28.

Liang, Y., Duveneck, M. J., Gustafson, E. J., Serra-Diaz, J. M. and Thompson, J. R. 2018. How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. – Global Change Biol. 24: e335–e351.
Lister, B. C. and Garcia, A. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. – Proc. Natl Acad. Sci. USA. 115: E10397–E10406.
Luedtke, J. A. et al. 2023. Ongoing declines for the world's amphibians in the face of emerging threats. – Nature 622: 308–314.
Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L. and Zbinden, N. 2011. Are Swiss birds tracking climate change?: detecting elevational shifts using response curve shapes. – Ecol. Modell. 222: 21–32.
McAdam, A. G., Boutin, S., Sykes, A. K. and Humphries, M. M. 2007. Life histories of female red squirrels and their contributions to population growth and lifetime fitness. – Ecoscience 14: 362–369.
McGarigal, K., Cushman, S. A. and Stafford, S. 2013. Multivariate statistics for wildlife and ecology research. – Springer.
Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D. and Thorne, J. H. 2020. Climate-change refugia: biodiversity in the slow lane. – Front. Ecol. Environ. 18: 228–234.
Morelli, T. L., Hallworth, M. T., Duclos, T., Ells, A., Faccio, S., Foster, J. R., McFarland, K. P., Nislow, K., Ralston, J., Ratnaswamy, M., Deluca, W. V. and Siren, A. P. K. 2025. Data from: Does habitat or climate change drive species range shifts? – Dryad Digital Repository, https://doi.org/10.5061/dryad.qfttdz0q8.
Nogués-Bravo, D., Rodríguez-Sánchez, F., Orsini, L., de Boer, E., Jansson, R., Morlon, H., Fordham, D. A. and Jackson, S. T. 2018. Cracking the code of biodiversity responses to past climate change. – Trends Ecol. Evol. 33: 765–776.
Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.
Patterson, B. D., Ceballos, G., Sechrest, W., Tognelli, M. F., Brooks, T., Luna, L., Ortega, P., Salazar, I. and Young, B. E. 2007. Digital distribution maps of the mammals of the Western Hemisphere, ver. 3.0. – NaturServe.
Plummer, M. 2017. JAGS ver. 4.3.0 user manual. – SCRIBD.
Poniatowski, D., Beckmann, C., Löffler, F., Münsch, T., Helbing, F., Samways, M. J. and Fartmann, T. 2020. Relative impacts of land-use and climate change on grasshopper range shifts have changed over time. – Global Ecol. Biogeogr. 29: 2190–2202.
Rapacciuolo, G., Maher, S. P., Schneider, A. C., Hammond, T. T., Jabis, M. D., Walsh, R. E., Iknayan, K. J., Walden, G. K., Oldfather, M. F., Ackerly, D. D. and Beissinger, S. R. 2024. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. – Global Change Biol. 20: 2841–2855.
Réale, D., McAdam, A. G., Boutin, S. and Berteaux, D. 2003. Genetic and plastic responses of a northern mammal to climate change. – Proc. R. Soc. B 270: 591–596.
Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M. and Marra, P. P. 2019. Decline of the North American avifauna. – Science 366: 120 –124.
Rosseel, Y. 2012. lavaan: an R package for structural equation modeling. – J. Stat. Softw. 48: 1–36.
Rossi, A. J., Klinger, R. C., Hellwig, E. C. and Van Vuren, D. H. 2023. Niches of three sympatric montane ground-dwelling squirrels: relative importance of climate, topography, and land-cover. – Ecol. Evol. 13: e9949.
Rowe, K. C., Rowe, K. M. C., Tingley, M. W., Koo, M. S., Patton, J. L., Conroy, C. J., Perrine, J. D., Beissinger, S. R. and Moritz, C. 2015. Spatially heterogeneous impact of climate change on small mammals of montane California. – Proc. R. Soc. B 282: 20141857.
Rubenstein, M. A., Weiskopf, S. R., Bertrand, R., Carter, S. L., Comte, L., Eaton, M. J., Johnson, C. G., Lenoir, J., Lynch, A. J., Miller, B. W., Morelli, T. L., Rodriguez, M. A., Terando, A. and Thompson, L. M. 2023. Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. – Environ. Evid. 12: 7.
Rusch, D. A. and Reeder, W. G. 1978. Population ecology of Alberta red squirrels. – Ecology 59: 400–420.
Sánchez-Bayo, F. and Wyckhuys, K. A. G. 2019. Worldwide decline of the entomofauna: a review of its drivers. – Biol. Conserv. 232: 8–27.
Satorra, A. and Bentler, P. M. 1994. Corrections to test statistics and standard errors in covariance structure analysis. – In: Eye, A. Von. and Clogg, C. C. (eds), Latent variable analysis: applications for developmental research. – Sage, pp. 399–419.
Shipley, B. 2016. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. – Cambridge Univ. Press.
Sirén, A. P. K. and Morelli, T. L. 2020. Interactive range-limit theory (iRLT): an extension for predicting range shifts. – J. Anim. Ecol. 89: 940–954.
Sirén, A. P. K., Sutherland, C. S., Karmalkar, A. V., Duveneck, M. J. and Morelli, T. L. 2022. Forecasting species distributions: correlation does not equal causation. – Divers. Distrib. 28: 756–769.
Sittaro, F., Paquette, A., Messier, C. and Nock, C. A. 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. – Global Change Biol. 23: 3292–3301.
Slauson, K. M. and Zielinski, W. J. 2017. Seasonal specialization in diet of the Humboldt marten (*Martes caurina humboldtensis*) in California and the importance of prey size. – J. Mammal. 98: 1697–1708.
Staudinger, M. D., Karmalkar, A. V., Terwilliger, K., Burgio, K., Lubeck, A., Higgins, H., Rice, T., Morelli, T. L. and D'Amato., A. 2024. A regional synthesis of climate data to inform the 2025 State Wildlife Action Plans in the Northeast US. – Northeast Climate Adaptation Science Center Cooperator Report. doi.org/10.21429/t352-9q86.
Stralberg, D., Bayne, E. M., Cumming, S. G., Sólymos, P., Song, S. J. and Schmiegelow, F. K. A. 2015. Conservation of future boreal forest bird communities considering lags in vegetation response to climate change: a modified refugia approach. – Divers. Distrib. 21: 1112–1128.
Thompson, J. R., Carpenter, D. N., Cogbill, C. V. and Foster, D. R. 2013. Four centuries of change in northeastern United States forests. – PLoS One 8: e72540.
Tingley, M. W., Koo, M. S., Moritz, C., Rush, A. C. and Beissinger, S. R. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. – Global Change Biol. 18: 3279–3290.
Turkia, T., Selonen, V., Danilov, P., Kurhinen, J., Ovaskainen, O., Rintala, J. and Brommer, J. E. 2018. Red squirrels decline in

abundance in the boreal forests of Finland and NW Russia. – Ecography 41: 1370–1379.
Urban, M. C. et al. 2016. Improving the forecast for biodiversity under climate change. – Science 353: aad8466.
Van Tatenhove, A., Filiberti, E., Sillett, T. S., Rodenhouse, N. and Hallworth, M. 2019. Climate-related distribution shifts of migratory songbirds and sciurids in the White Mountain National Forest. – Forests 10: 84.
Wang, T., Hamann, A., Spittlehouse, D. and Carroll, C. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. – PLoS One 11: e0156720.
Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., Morelli, T. L., Morisette, J. T., Muñoz, R. C., Pershing, A. J., Peterson, D. L., Poudel, R., Staudinger, M. D., Sutton-Grier, A. E., Thompson, L., Vose, J., Weltzin, J. F. and Whyte, K. P. 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. – Sci. Total Environ. 733: 137782.
Zimova, M., Giery, S. T., Newey, S., Nowak, J. J., Spencer, M. and Mills, L. S. 2020. Lack of phenological shift leads to increased camouflage mismatch in mountain hares. – Proc. R. Soc. B 287: 20201786.
Zuckerberg, B., Porter, W. F. and Corwin, K. 2009. The consistency and stability of abundance–occupancy relationships in large-scale population dynamics. – J. Anim. Ecol. 78: 172–181.