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Research article

A Great Escape: resource availability and density-dependence shape population dynamics along trailing range edges

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Populations along geographical range limits are often exposed to unsuitable climate and low resource availability relative to core populations. As such, there has been a renewed focus on understanding the factors that determine range limits to better predict how species will respond to global change. Using recent theory on range limits and classical understanding of density dependence, we evaluated the influence of resource availability on the snowshoe hare *Lepus americanus* along its trailing range edge. We estimated variation in population density, habitat use, survival, and parasite loads to test the Great Escape Hypothesis (GEH), i.e. that density dependence determines, in part, a species' persistence along trailing edges. We found that variability in resource availability affected density and population fluctuations and led to trade-offs in survival for snowshoe hare populations in the northeastern USA. Hares living in resource-limited environments had lower and less variable population density, yet higher survival and lower parasitism compared to populations living in resource-rich environments. We suggest that density-dependent dynamics, elicited by resource availability, provide hares a unique survival advantage and partly explain persistence along their trailing edge. We hypothesize that this low-density escape from predation and parasitism occurs for other prey species along trailing edges, but the extent to which it occurs is likely conditional on the quality of matrix habitat. Our work indicates that biotic factors play an important role in shaping species' trailing edges and more detailed examination of non-climatic factors is warranted to better inform conservation and management decisions.

Keywords: climate change, density dependence, *Lepus americanus*, predation, range-limits, resource availability

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Introduction

Understanding the causes of range limits is a fundamental theme in ecology and evolution (Connallon and Sgrò 2018). Although climate is often considered an ultimate determinant of range limits, the role of biotic interactions can be equally important and is often a direct limiting factor, especially for populations along trailing edges (Louthan et al. 2015, Sirén and Morelli 2020). Previous research has focused more on the role of competition whereas less attention has been given to predation, parasitism and resource-mediated density dependence (Holt and Barfield 2009). Furthermore, abiotic stress and resource availability can mediate biotic interactions and affect trophic levels differently, resulting in divergent population dynamics along distributional edges (Sirén and Morelli 2020). These trophic differences are important to consider given that current and projected changes in climate and resource availability will likely have profound effects on trailing edge populations (Hampe and Petit 2005).

For mammalian herbivores that are more limited by predation or parasitism than competition along trailing edges (reviewed by Sirén and Morelli 2020), variations in climate and resource availability can influence population dynamics and thus vulnerability to predation and parasitism. For example, high density moose *Alces alces* populations are negatively affected by a warming climate through elevated levels of parasitism or disease (Murray et al. 2006, Ellingwood et al. 2020). However, variations in resource availability can influence host density and infestations (Samuel 2007) that potentially explains why some low-density moose populations persist at range edges (Samuel 2007, Wattles and DeStefano 2011). Despite examples of this dynamic occurring in other systems at local scales (Reznick et al. 2004, Griffen and Williamson 2008), the influence of climate and resource availability on density-dependent dynamics is rarely examined at broader spatial scales.

Abiotic stress (e.g. deep snow) has been shown to mediate negative biotic interactions for wildlife populations along lower range limits (Sirén and Morelli 2020). However, existence at low density, mediated by low resource availability (i.e. a bottom-up process), may provide herbivores a refuge from predation and parasitism, and facilitate an escape from these biotic interactions along their lower limits (Sirén and Morelli 2020). Hereafter we refer to this rarely explored idea, that density dependence determines, in part, a species' persistence along trailing edges, as the Great Escape Hypothesis (GEH). It is similar to Janzen–Connell effects (reviewed by Comita et al. 2014) but applied to primary consumers at regional and biogeographic scales. Briefly, Janzen–Connell effects are density- or distance-dependent processes that explain predation of seeds/seedlings by specialist predators at local scales; seeds/seedlings in areas of low seed density or farther away from a parent plant have higher survival (Comita et al. 2014). The density-dependent hypothesis of Janzen–Connell effects (i.e. the Escape Hypothesis: Howe and Smallwood 1982) is akin to a type III functional response associated with generalist predators (Holling 1959, Oaten and Murdoch 1975); specialist predators are able to hunt their prey to very low numbers but at the detriment of their own survival (type II functional response), but generalist predators prey-switch when densities of a particular prey become too low (type III functional response), allowing low-density prey to escape predation. Thus, the GEH is similar to the Escape Hypothesis, except that it also includes upper trophic levels and focuses on biogeographic processes, hence the name 'Great Escape'.

There are several assumptions and conditions that underpin the GEH. First, the GEH assumes that populations living in resource-limited environments will exist at lower densities but have higher survival due to density-dependent predation (sensu Holling 1959), although the latter may be contingent on the quality of matrix habitat (Sirén and Morelli 2020). Consequently, populations living in resource-poor areas will not vary (temporally) as much as those in resource-rich environments that exist at higher densities and attract more predators (Hendry 2017). Second, the availability of resources for trailing edge populations is more patchily distributed or fragmented than in the core of the species range (Hampe and Petit 2005), resulting in lower occupancy and abundance (Pironon et al. 2017). Lastly, density-dependent processes, commonly evaluated by community ecologists at local scales, are consistent across several spatial scales (i.e. local, landscape, regional and biogeographical). In summary, the combination of resource availability and density-dependent dynamics will allow prey species to escape predation and persist at lower latitudes than their specialist predators (Sirén and Morelli 2020). Although there is support in the literature for predictions of the GEH, especially within aquatic ecosystems (Seitz et al. 2001, Griffen and Williamson 2008), its predictions have yet to be explicitly tested empirically.

We tested the GEH in snowshoe hares *Lepus americanus*, using field data collected during a five year period (2015–2019) in the northeastern USA. Snowshoe hares are a primary prey species for many carnivores in North America and have been the focus of intensive ecological study over the past century (Krebs et al. 2001). They are a model organism for understanding population dynamics and how snow-adapted species might respond to climate change (Griffin and Mills 2009, Mills et al. 2013, 2018, Zimova et al. 2020). In particular, hares experience divergent pressures due to variable climate and resource availability and often live in the absence of specialist predators along the trailing (southern) edge of their range (Wirsing et al. 2002, Sultaire et al. 2016, Burt et al. 2017, Gigliotti and Diefenbach 2018, Sirén et al. 2021). Identifying mechanisms influencing the demography of range-edge populations of hares may provide information for how other prey species respond to climate and land-use change.

The focus of this study was to evaluate the GEH by comparing demographic parameters among populations of snowshoe hares along their range edge in the northeastern USA. Accordingly, we hypothesized that resource availability (early-regenerating forest) would exert a strong bottom-up effect on the abundance of hares (Litvaitis et al. 1985b, Holbrook et al.

2017) and influence space use (Andreassen et al. 1998), yet this would elicit density-dependent predation. Following this logic, we predicted that hares would have higher survival (despite low resources and longer movements; Ims et al. 1993) due to density-dependent predation by generalist carnivores that are common along the southern edge of the range of snowshoe hares (Chan et al. 2017, Sirén et al. 2021). Accordingly, we predicted that hare populations would not vary (temporally) as much in these environments due to a low-density refuge from generalist predators driven by low resource availability. We further evaluated the GEH by comparing parasite loads of rabbit ticks *Haemaphysalis leporispalustris* between populations living in high- and low-resource environments. Ultimately, we hypothesized that a combination of climate and resource conditions, as well as the presence of generalist predators, allows hares to persist along the trailing edge of their range in the northeastern USA (Table 1).

Material and methods

Study area

Our study area was in the northeastern USA within the states of New Hampshire and Vermont (Fig. 1). This area is part of the northern hardwood and boreal forest transition zone (Goldblum and Rigg 2010) and includes the highest peaks of the northeastern USA. Boreal forest is generally found at higher elevations and latitudes. The climate of the region is maritime with mild and rainy summers and cold winters with variable snowpack (McNab et al. 2007). Annual snowfall and temperature varies considerably, with deeper snow and colder temperatures at high elevations and northern regions (Table 2; Abatzoglou 2013, Livneh et al. 2015).

Predators of hares in the study area included generalist species (coyotes *Canis latrans*, bobcats *Lynx rufus*, red fox *Vulpes vulpes*, fisher *Pekania pennanti*, American marten *Martes americana*, weasels *Mustela* spp., northern goshawks *Accipiter gentilis*, and great-horned owls *Bubo virginianus*) and one specialist (Canada lynx *Lynx canadensis*). Generalist predators typically were widespread, except for bobcats that occupied lower elevation and southern regions and martens that were primarily distributed in northern and high elevation regions (Sirén et al. 2021, 2022). Lynx were common only in the northernmost region (Connecticut Lakes) of the study area (Sirén et al. 2021, 2022) and occurred at low density.

To evaluate the GEH, we sampled a variety of conditions that snowshoe hares experience, choosing 3 different landscapes (White Mountain National Forest [WMNF], Nulhegan Basin [NB], Connecticut Lakes [CL]) that varied in snowpack and resource (habitat) availability (Table 2, Fig. 1). The WMNF was the southernmost and highest elevation landscape (Table 2, Fig. 1), containing some of the oldest forests and deepest snowpack in the northeastern USA (Seidel et al. 2009, Foster and D'Amato 2015). Consequently, we considered the WMNF to be the low-resource landscape, as older forest is not considered prime habitat for hares in eastern North America (Homyack et al. 2007, Hodson et al. 2011, Sirén et al. 2021). NB was the mid-latitude and lowest elevation landscape (Table 2). It was dominated by spruce (*Picea* spp.)-balsam fir *Abies balsamea* forest that had been extensively harvested following the spruce-budworm *Choristoneura fumiferana* epidemic in the 1970s and 1980s (Simons-Legaard et al. 2013). It had the shortest snow duration and shallowest depths compared to the WMNF and CL (Table 2). The CL was the northernmost and mid-elevation study landscape. It was similar to the NB in forest composition and age yet had deep snow and long winters like the

Table 1. Description of hypotheses, predictions, and data used to evaluate the influence of resource availability on snowshoe hare demography.

Demographic parameter	Hypotheses	Predictions	Data source
Density	Forest age would influence resource availability (food, thermoregulation, protection from predators) and influence hare densities	Density would be positively associated with early-regenerating boreal forest stands and landscapes	Fecal pellet surveys and live-trap data collected from 2015–2019 in the CL, NB, and WMNF. Pellet data were used as an index of abundance and live-trap data were used to estimate density using spatial capture-recapture models
Population fluctuations	The quality and amount of habitat would influence snowshoe hare population fluctuations because of density-dependent dynamics	Population densities would vary more in resource-rich environments (early-regenerating boreal forest)	Annual fecal pellet surveys (index of abundance) collected from 2015–2019 in the CL, NB, and WMNF landscapes
Survival	The quality and amount of habitat would influence snowshoe hare survival because of density-dependent dynamics	Hare survival would be lower in the resource-rich environments due to density-dependent dynamics	Survival data collected from radio-collared snowshoe hares from 2016–2018 in the NB and WMNF. Known fates of hares were used to model survival
Space use	The movements and size of home ranges would reflect habitat quality and resource availability	Movements would be shorter in resource-rich environments	Telemetry relocation and live-trap data collected from radio-collared hares during the summer of 2016 in the NB and WMNF
Parasitism	Parasitism would be associated with resource availability and density-dependence	Parasitism would be higher in resource-rich environments due to density-dependent dynamics	Presence of ticks on the ears of hares captured from live-trapping during the summers of 2016–2017 in the NB and WMNF

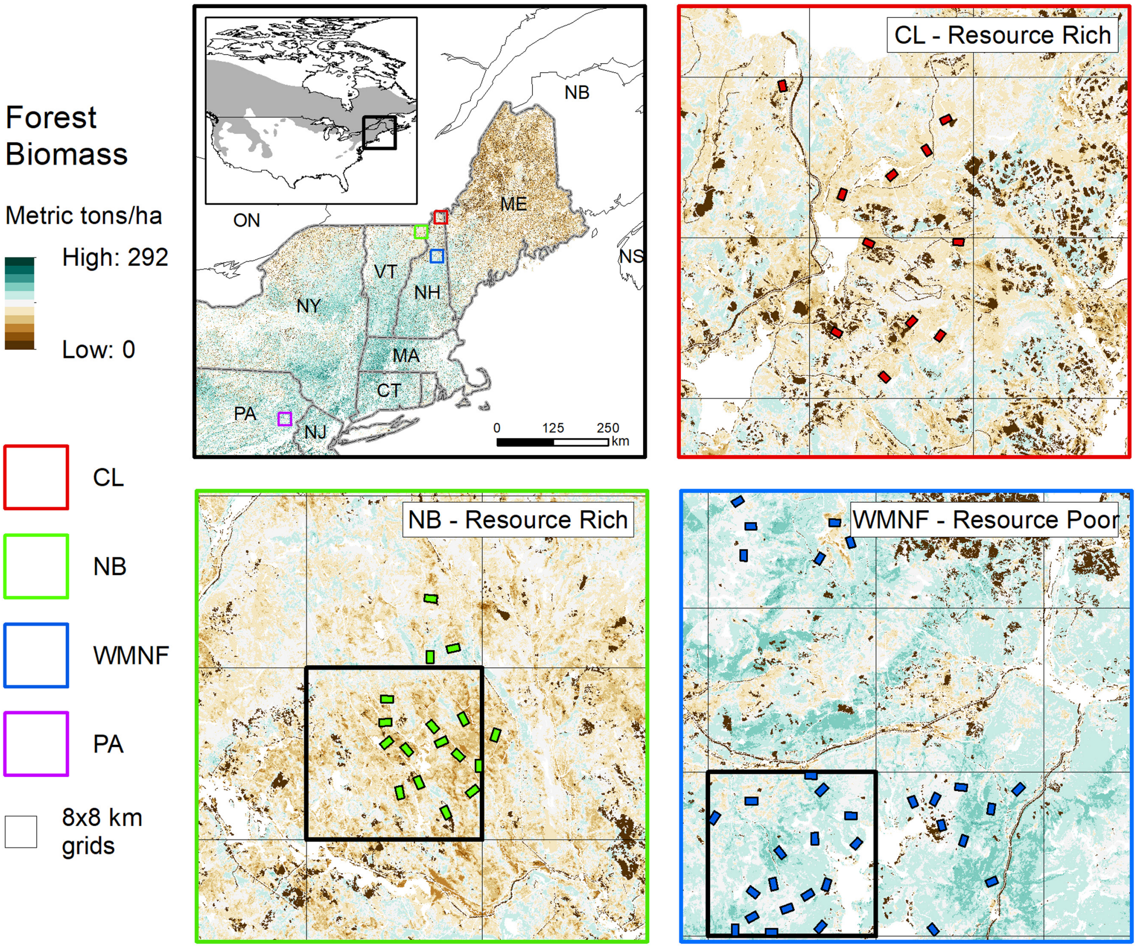

Figure 1. Location of the study area and landscapes (upper left panel) for evaluating snowshoe hare demography in the northeastern USA, including a recent study in Pennsylvania (Gigliotti 2016; purple polygon). The snowshoe hare range map (gray; upper left panel inset) was downloaded from the IUCN (ver. 2020–2, https://www.iucnredlist.org) on 10 November 2020. The CL (red; Connecticut Lakes), NB (green; Nulhegan Basin), and WMNF (blue; White Mountain National Forest) landscapes were sampled to evaluate density, population fluctuations, and survival. Colored rectangles indicate stands (n = 60) used for estimating relative density via the pellet-plot method and the bold black 8 x 8 km grids outline the NB and WMNF telemetry study landscapes. Brown to blue color gradient indicates forest biomass used here as a proxy for resource availability (Sirén et al. 2021) with browner colors showing resource rich (low biomass) areas and bluer colors showing resource poor (high biomass) areas.

Table 2. Mean (SD) latitude, elevation, and climate (1980–2009) of the study landscapes (WMNF, NB, CL) and the duration (biological years, ending in mid-May) of field efforts (Fecal pellet surveys, Live-trapping and radio-collaring) for evaluating relative density, absolute density, space use, parasitism, and survival of snowshoe hares.

Landscape[a]	Latitude (°N)	Elevation (m)	Temp (°C)[b]	Snow duration (days)[c]	SWE (cm)[c]	Fecal pellet surveys	Live-trapping and radio-collaring[d]
WMNF	44.34 (0.05)	836.91 (273.35)	4.25 (10.59)	187 (70)	110 (32)	4 (2015–2018)	2 (2016–2017)
NB	44.84 (0.02)	422.75 (61.05)	4.44 (11.34)	148 (67)	52 (18)	4 (2016–2019)	2 (2016–2017)
CL	45.16 (0.04)	712.00 (125.02)	3.14 (11.35)	184 (65)	115 (24)	2 (2018–2019)	-

[a]Landscapes are abbreviated as follows: WMNF = White Mountain National Forest; NB = Nulhegan Basin; CL = Connecticut Lakes. [b]Temperature data (average annual values within each landscape) were obtained from gridMET (Abatzoglou 2013). [c]Snow duration and snow water equivalent (SWE) data (average annual values within each landscape) were obtained from Livneh et al. (2015). [d]Telemetered animals captured and radio-collared in 2016 and 2017 were monitored through 2018.

WMNF landscape (Table 2). We a priori considered the CL and NB to be resource-rich landscapes as low biomass (i.e. early-regenerating) forests have a strong positive effect on hare occupancy in the northeastern USA (Sirén et al. 2021) and forest biomass is clearly lower in the CL and NB landscapes (Fig. 1).

We monitored hare populations in all three landscapes using fecal pellet surveys to index relative density (Litvaitis et al. 1985a, Hodges and Mills 2008) and evaluate population fluctuations, sampling 60 stands that were representative of each landscape and the entire study area (Table 1, 2, Fig. 1). We chose two of these landscapes (WMNF, NB) to live-trap and radio-collar hares to 1) estimate landscape-scale density, 2) obtain telemetry locations for evaluating space use, 3) compare differences in parasite loads between populations and 4) identify factors influencing survival (Table 1, 2, Fig. 1).

Live-trapping and radio-collaring

We live-trapped and radio-collared hares from 20 June–13 August 2016 and the following year from 6 June–28 July 2017. We placed live-traps ($n = 25$–50) approximately 50 m apart, within 5 m of pellet plots (next section), baited traps with alfalfa and apple slices, and used vanilla extract as a lure. Upon capture, hares were sexed, ear-tagged, and radio-collared with lightweight (26 g) VHF collars (ATS, Isanti, Minnesota, USA); only adults were processed (juveniles were differentiated using hind foot measurements; Litvaitis, 1990). All activities associated with trapping, handling, and radio-collaring followed an animal care and use protocol (Sikes 2016) that was approved by the University of Massachusetts, Amherst.

Fecal pellet surveys

To evaluate relative density and population fluctuations, we established snowshoe hare fecal pellet plots within forested stands in the WMNF, NB and CL landscapes (Fig. 1). We chose fecal pellet surveys as they are an effective approach to monitor hares over broad spatial and temporal extents; additionally many studies, including our own work, have found a strong positive correlation between pellet counts and hare density (Mills et al. 2005, Homyack et al. 2006, Berg and Gese 2010, Sirén 2020). We selected stand types based on purported high density of hares (lowland and montane spruce-fir) and those common in the region (northern hardwood spruce-fir [mixedwood], and northern hardwood forest [hardwood]) using a forest classification system for the region (Sperduto and Nichols 2012). We selected stands that were of similar age classes as hare density is influenced by a broad spectrum of seral stages (Hodson et al. 2011); the range of age for stands was 20–40 years (early-regenerating), 41–70 years (mid-regenerating), and 89–295 years (late-regenerating/mature). Our classification scheme of stand types and seral classes resulted in 14 early-regenerating stands (2 hardwood and 12 lowland spruce-fir) and three late-regenerating mixedwood stands in the NB, six early-regenerating and five mid-regenerating lowland spruce-fir stands in the CL, and 32 late-regenerating stands in the WMNF (15 montane spruce-fir, 7 mixedwood, 6 lowland spruce-fir and 4 hardwood).

Stands were either 18 (540 × 340 m) or 20 ha (590 × 340 m), including a 70 m buffer to reduce edge effects (Newbury and Simon 2005), and spaced > 500 m apart to meet assumptions of independence, as average space use and mean dispersal distances are less than this threshold (Homyack et al. 2006, Griffin and Mills 2009). Each stand contained five parallel transects with 9–10 plots all spaced 50 m apart, resulting in 45–50 plots / stand.

Pellet plots were counted and cleared biannually (starting one season after they were initially cleared) to index leaf-off (16 October–15 May) density (Table 2). We only used pellet plot data from the leaf-off period because it is more correlated with density of adults that survived the previous winter (Homyack et al. 2006). Pellets were counted and cleared within a 56 cm radius circular plot (Murray et al. 2002, Hodges and Mills 2008).

Stand- and landscape-scale density

We used pellet data from 60 stands to evaluate stand- and landscape-scale relative density. We modeled pellet counts using a negative binomial generalized linear mixed model (GLMM) with a log link function using the 'glmmTMB' package in R (Brooks et al. 2017, www.r-project.org). We chose a negative binomial probability distribution because it is well-suited for aggregated count data with a high number of zeros (O'Hara and Kotze 2010). For each model, we included the 'stand' and 'plot' as a nested random effect to account for potential spatial correlation between stands and plots. Additionally, 'year' was included as a random effect for the landscape scale models. To account for differences in accumulation rates since the time plots were last sampled, we fit the log number of days since clearing ('day') as an offset variable.

We modeled counts (adjusted for time) as a function of stand and landscape type; landscapes were defined as all the stands within a landscape (i.e. WMNF, NB and CL). We made comparisons between stand- and landscape-levels using Tukey-adjusted tests with the 'emmeans' package in R (www.r-project.org, Lenth et al. 2023). Finally, we also evaluated spatial autocorrelation of model residuals (rSAC) using a Moran's-I test and evaluated significance at the 95% confidence level. Because we detected rSAC for stand and landscape models, we fit an exponential spatial covariate that incorporated the locations of each plot. We chose the exponential correlation structure because other terms failed to converge (e.g. Gaussian, Matern) and subsequent Moran's-I tests revealed that this covariate greatly reduced issues of rSAC.

We also evaluated differences in absolute hare density between the NB and WMNF landscapes, fitting spatial capture-recapture (SCR) models (Royle et al. 2018) from the spatial capture histories of individuals captured during live-trapping. We only used data from 2016 as our live-trapping efforts were more comprehensive during that season. First, we evaluated factors influencing baseline encounter probability ($\rho0$) and space use (σ) using an AIC-based approach and chose the best combination of variables to evaluate density (d) (Sutherland et al. 2019). During each step, we held the other parameters at their null value (e.g. hold σ and d at '1' while allowing p0 to vary) and considered the model with the lowest AIC score as the top model. For $\rho0$, we considered a trap-specific behavioral response, 'landscape', and 'sex', and evaluated abiotic ('temperature', 'precipitation') and temporal ('Julian day', 'Julian day^2') variables. We evaluated σ using only 'landscape' and 'sex'. Once we determined the best models for $\rho0$ and σ, we evaluated d using 'landscape' to obtain density estimates (hares/ha) for each landscape (WMNF, NB). We also estimated population sizes of each landscape by multiplying density estimates by the area of the 8 ×8 km grids (6400 ha) that encompassed and represented all stands in each landscape (Fig. 1). All SCR analyses were performed using the oSCR package in R (www.r-project.org, Sutherland et al. 2019).

Population fluctuations

To evaluate annual population fluctuations for each landscape (Table 2 for sample sizes), we employed the same modeling approach used to evaluate bottom-up factors on relative hare density (i.e. a negative binomial GLMM), except we included 'year' as a fixed effect to evaluate differences in years. Further, because we found evidence of residual spatial autocorrelation (i.e. rSAC) for these models, we also included an exponential term to account for correlated errors and resolved issues of rSAC. To compare relative differences in population variability among landscapes, we calculated the coefficient of variation (Gaston and McArdle 1994), expressed as a percent ($CV = variance / mean \times 100$); variance ($\sigma^2$) was calculated using the overdispersion parameter (θ) from the negative binomial model that uses a quadratic parameterization ($\sigma^2 = \mu + \mu^2 / \theta$) and means ($\mu$) were obtained from the 'emmeans' package.

Space use

To evaluate our prediction that low resource availability in the WMNF landscape would result in longer movements, we conducted telemetry monitoring on a weekly basis during the leaf-on season (16 May – 15 October) of 2016. Every effort was made to obtain at least one location per week for each individual and to prevent location biases by sampling at different times of the day. We obtained locations via triangulation, homing and visual observations, and in a few cases biangulation using a standard telemetry protocol (Sirén et al. 2016). We used telemetry software (LOAS; Ecological Software Solutions, Hegymagas, Hungary) to estimate locations using a maximum likelihood method and the 'adehabitatHR' package (Calenge et al. 2009) to calculate the distance moved (m) between successive locations. To compare differences in the mean distance moved between the NB and WMNF, we performed a one-way analysis of variance using the 'glmmTMB' R package (www.r-project.org, Brooks et al. 2017). We log-transformed distances to meet assumptions of normality and specified individual hares as a random effect to account for repeated measurements. We also evaluated differences in space use between landscapes using the movement parameter (i.e. σ) from the SCR model.

Parasitism

We recorded the presence of rabbit ticks *H. leporispalustris* by inspecting the ears of each captured individual (Keith and Cary 1990) and used a Fisher's-exact test to compare frequencies of animals with ticks present between landscapes; alpha was set at 0.05 and the test was performed using the 'fisher.test' function in R (www.r-project.org). Our analysis included 79 records (NB = 59, WMNF = 20), including five hares that were captured during both years of trapping, resulting in five more records than the total number of unique hares captured during the study (NB = 57, WMNF = 17).

Survival

To evaluate differences in survival rates between landscapes, we monitored radio-collared hares weekly within six and five stands in the NB and WMNF, respectively, that spanned the density of hares for each landscape. When possible, cause-specific mortality was assessed via necropsy, and we determined cause of death for each mortality following a standard protocol (Supporting information).

We monitored hare survival weekly over a two-year period (16 May 2016 – 15 May 2017; 16 May 2017 – 15 May 2018). We chose this annual calendar because it corresponded with the timing of our trapping efforts. We fit a Cox regression model with the R package 'survival' (Therneau and Lumley 2017, www.r-project.org) to compare weekly survival rates between the NB and WMNF. We evaluated the significance of parameter estimates at the 95% confidence level. Further, we tested for violations of proportional hazards with a χ^2 test using the 'survival' package, where a $p < 0.05$ indicates a violation of proportionality and poor fit (Therneau and Lumley 2017).

Results

Live-trapping and radio-collaring

We live-trapped adult snowshoe hares in five stands in the NB during the summer of 2016, capturing 38 adults (21 M; 17 F) 71 times (n = 33 recaptures; Supporting information). During the summer of 2017, we trapped in three stands, including one that was trapped the previous summer (9SFF4, 9SFF6, 9SFU1; Supporting information), capturing 22 adults (12 M; 10 F) 54 times (n = 32 recaptures).

We trapped in seven stands in the WMNF (Supporting information) during the summer of 2016, capturing 14 adults (7 M; 7 F) 24 times (n = 10 recaptures). During the summer of 2017, we trapped in two stands from the previous summer (6HSF3, 6SFW1; Supporting information) and captured six adults (2 M; 4 F) 12 times (n = 6 recaptures).

Fecal pellet surveys

During spring and fall surveys from 2015–2019, we counted and cleared 839 pellet plots in 17 stands in the NB, 1535 plots in 32 stands in the WMNF and 495 plots in 11 stands in the CL landscape (Supporting information).

Stand- and landscape-scale density

Relative hare density, as indexed using pellet data, was significantly higher in the early-regenerating conifer-dominated stands of the NB and CL compared to all other stand types (Fig. 2, Supporting information), with most stands in the WMNF having low pellet density (Supporting information). Accordingly, landscape-scale density was significantly lower ($p < 0.05$) in the WMNF compared to the NB and CL (Fig. 2 inset, Supporting information). However, although relative density was higher in the NB than the CL, these differences were not significant (Fig. 2 inset, Supporting information).

The top SCR model for estimating landscape-scale density indicated sex- and landscape-specific differences in encounter probability, behavior responses, and density. Encounter probability was significantly lower for males than females (Supporting information). We also found evidence for a strong positive trap-specific response, indicating hares were more likely to enter traps after their first encounter (Supporting information). Landscape-density estimates were significantly higher ($p = 0.008$) in the NB (0.36 hares / ha) than the WMNF (0.08 hares / ha; Supporting information).

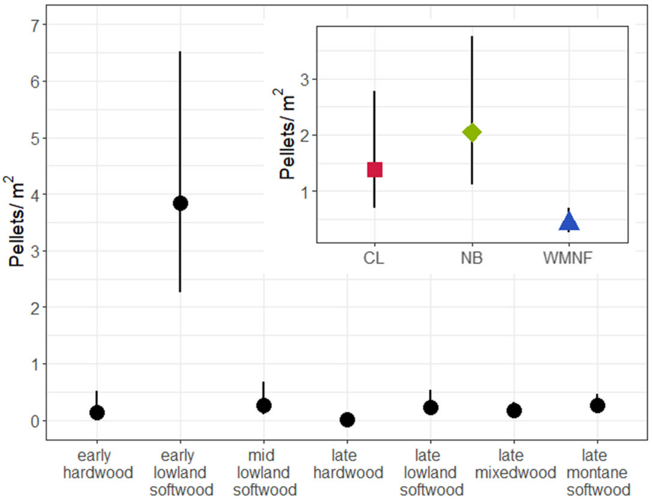

Figure 2. Mean snowshoe hare density (pellets / m^2) for seven forest types in the NB, CL, and WMNF and for each landscape (inset), using pellet data collected from 2015–2019. Vertical bars show 95% confidence intervals. Note, the error bars are not visible for some stands due to very small confidence intervals.

Accordingly, population estimates for each 8 x 8 km landscape (64 km^2) were 2304 and 512 hares in the NB and WMNF, respectively.

Population fluctuations

We detected differences in population fluctuations among landscapes. Comparatively, relative density remained low and stable in the WMNF yet fluctuated greatly in the NB and CL (Fig. 3). Specifically, annual CV were generally lower in the WMNF (165–190%) compared to the CL and NB (178–292%) landscapes (Fig. 3 inset). Of note, there were only two annual CV estimates for the CL landscape and the uncertainty of annual density estimates was higher in this landscape due to a mixture of early- and mid-regenerating stands and lower sample sizes (Fig. 3).

Space use

We evaluated space use of telemetered animals and movements between live traps as an indicator of habitat quality and the distribution of optimal habitat. We radio-collared 30 hares in the NB and 12 in the WMNF during the leaf-on season of 2016 (16 May – 15 October). We recorded 206 locations (6.9 ± 0.3 SE locations / hare) and 97 locations (8.1 ± 0.7 SE locations / hare) in the NB and WMNF, respectively, obtaining locations on successive weeks half of the time (50 ± 3% SE; range = 15–100%). Mean distance moved between successive locations was significantly longer in the WMNF (248 ± 29 m; log-transformed $\beta = 0.488 \pm 0.15$, $p = 0.001$) than the NB (156 ± 10 m), even after

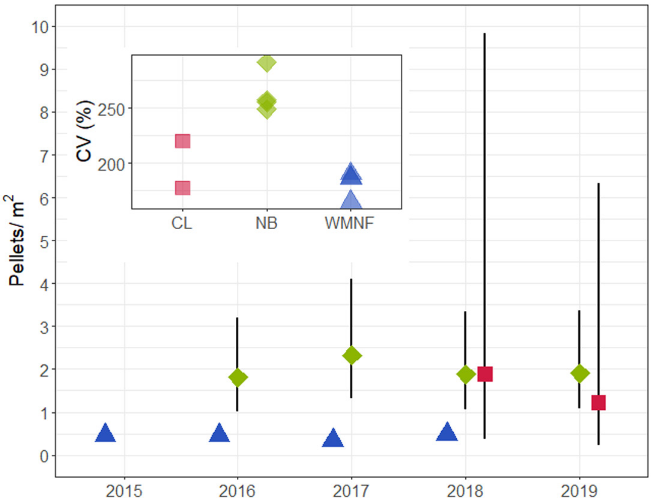

Figure 3. Annual variation in mean snowshoe hare density (pellets / m^2) in the CL, NB, and WMNF landscapes from 2015–2019 as indexed using data from pellet surveys. Vertical bars show 95% confidence intervals and are not visible for the WMNF due to very small confidence intervals. Inset plot shows the relationship between expected values (μ) and variance (σ^2) for each landscape and year. Annual CV ($\sigma^2 / \mu \times 100$) were generally lower in the WMNF compared to the NB and CL landscapes, indicating lower population variability.

accounting for telemetry error (21.5 ± 4.7 m; Supporting information). Further, movements between live traps, as estimated using SCR models, were marginally longer ($p = 0.053$) in the WMNF (166 ± 37 m) than the NB (98 ± 15 m; Supporting information).

Parasitism

During the two years of live-trapping and capture, we detected numerous rabbit ticks on each hare in the NB (59 of 59 [100%] hares, including two captured during both years, had ticks), but only counted one tick on one individual in the WMNF (1 of 20 [5%] hares, including three captured during both years, had ticks). Accordingly, the prevalence of ticks on hares was significantly higher ($p < 0.0001$) in the NB.

Survival

We monitored a total of 63 adult hares from 21 June 2016–15 May 2018. One female hare from the NB was censored due to collar failure, resulting in 62 hares for the survival analysis. The proportion of hares surviving the entire study was considerably lower for the NB (17%; 8 of 48 animals alive) than the WMNF (50%; 7 of 14 animals alive). Accordingly, weekly survival was significantly higher in the WMNF ($\beta = -1.004$, $z = -2.439$, $p = 0.0147$; Fig. 4) with 75 and 64% of hares surviving compared to 37 and 28% in the NB during 2016 and 2017, respectively. Tests for violations of proportionality indicated that the model fit the data well ($\chi^2 = 0.03$, $p = 0.86$). Predation was the primary cause of mortality for both landscapes (62%; 29 of 47 mortalities; Supporting information). Further, many of the mortalities that were categorized as unknown were likely due to predation. However, we had inconclusive evidence (e.g. a few tufts of hair or bone fragments) to classify these mortalities as predation. Most predation events were associated with terrestrial predators with few attributed to avian predation (Supporting information). Finally, we identified the predator species (all generalists; two coyotes, two fisher, one marten and one bobcat) on six occasions and the taxonomic family of the predator on a further three occasions (Supporting information).

Discussion

Biotic interactions have long been considered a limiting factor for animal and plant populations along trailing edges (Darwin 1859, MacArthur 1984). This theory was recently extended to include predictions that abiotic stress can mediate biotic interactions and that the determining processes differ by trophic level (Sirén and Morelli 2020). For herbivores, more limited by predation or parasitism than competition (Hairston et al. 1960), density dependence plays an integral role and can potentially counteract negative biotic interactions when population sizes are low (Seitz et al. 2001). We hypothesized that this dynamic extends to macroecological scales (i.e. the GEH) and explains why the trailing edges of some herbivore species extend beyond the range of their natural enemies (Sirén and Morelli 2020). By integrating multiple data sources at different spatial scales collected over the same time frame, we show that density-dependent dynamics, likely mediated by resource availability, have an important role for sustaining populations along trailing edges, supporting the GEH.

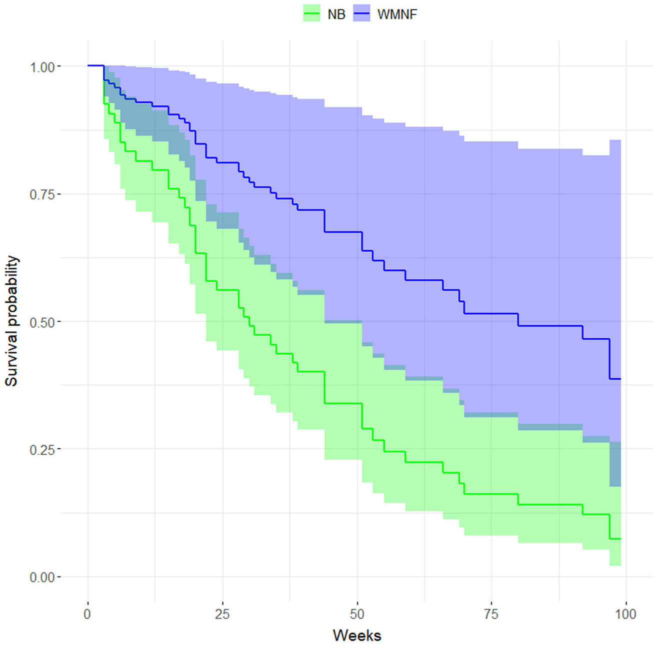

Figure 4. Weekly snowshoe hare survival at the NB and WMNF landscapes over a 100-week period. Estimates (fitted lines) and 95% confidence intervals (shaded regions) are from 62 individuals (NB = 48; WMNF = 14) of which 15 (NB = 8; WMNF = 7) remained at the end of the study.

Our previous work showed that forest biomass had a strong negative effect on snowshoe hare occupancy, indicating they were more likely to occur in early-regenerating forests in the northeastern USA (Sirén et al. 2021). At a local scale, it was evident that early-regenerating boreal forest was driving snowshoe hare density. These findings are in agreement with other studies in eastern North America that indicated early-regenerating stands dominated by spruce-fir provide optimal hare habitat (food and cover), likely due to dense horizontal and vertical cover afforded by conifer saplings (Buehler and Keith 1982, Litvaitis et al. 1985b). Indeed, the stands in the NB have more available browse than those in the WMNF (Courtot 2022). These structural forest attributes are found in a variety of seral stages, depending on region (Buehler and Keith 1982, Griffin and Mills 2009, Hodson et al. 2010) and influence broad scale patterns of occurrence and density (Lewis et al. 2011, Sultaire et al. 2016, Holbrook et al. 2017). However, as we discuss below, these resource-rich environments likely come with a cost.

Our hypothesis that populations living in low-resource environments would exist at lower densities, providing them a refuge from predation by generalist predators (i.e. the GEH), was well-supported. Hares were at lower density in the WMNF (i.e. the resource-limited landscape) and moved longer distances, presumably because of the patchy distribution of resources within this landscape (Courtot 2022). Further, there was no appreciable temporal variation in hare density in the WMNF, potentially remaining at carrying capacity (K) given the limited resources and absence of specialist predators. Consequently, this combination of factors likely contributed to higher survival compared to hares living in the resource-rich NB landscape. Although we expect that low mean densities would vary less (than high densities), we believe that our findings have a biological basis, as opposed to only being a statistical artifact, because of limited resources that influence both K and provide a low-density refuge from predation.

Adding support to the GEH, we only found a single rabbit tick on 1 of the 20 hares captured in the WMNF, whereas ticks were prevalent and often abundant on all 59 hares captured in the NB during the study. An alternative explanation for the lower mortality rates and near absence of ticks in the WMNF, other than density-dependence, was that winters were colder and snowier in the higher elevation WMNF compared to the NB. However, past studies found high mortality and parasitism of hares even in regions with long winters and deep snow (Campbell et al. 1980, Griffin and Mills 2009, Feierabend and Kielland 2015); all such populations were living in resource-rich environments. Furthermore, a recent study situated farther south of our sites found that hares had very high survival rates, despite large home ranges (Gigliotti 2016). Interestingly, this low-density population existed within a matrix of higher biomass forest, similar to the WMNF (Fig. 1, top left panel), yet milder climate. These findings bolster support for the GEH by adding an independent data point from a low-resource environment located even closer to the edge of the range of hares. Collectively, these findings provide support that bottom-up effects elicit density-dependent dynamics.

Our study provides an alternative explanation for dampened cycles in some parts of the snowshoe hare southern range. According to life-history theory, populations experiencing low predation pressure will often exhibit K-type traits such as lower reproductive output and stable population size (Hendry 2017). We found evidence of lower reproductive output in the resource-limited WMNF landscape (Sirén 2020) that had higher survival and lower population variability. We suggest that changes in life-history traits, caused by differences in resource availability and density-dependent predation (by generalists), may have a stabilizing effect on southern hare populations. While this hypothesis contrasts to the refugium model that draws from metapopulation dynamics (Wolff 1980, Griffin and Mills 2009), both support long-standing theory of dampened cycles at lower latitudes, via different causal pathways. The differences in demography between our study and those in the western USA (Wirsing et al. 2002, Griffin and Mills 2009, Kumar 2020) might be attributed to the quality of matrix habitat. Much of the boreal forest in the western USA is fragmented and surrounded by open habitat due to both natural heterogeneity and relatively recent logging (Griffin and Mills 2009), whereas boreal forest in the northeastern USA is intermixed with temperate forest (Goldblum and Rigg 2010) that is likely more suitable matrix habitat. As predicted by the GEH, these conditions may provide a low-density refuge from predators (Sirén and Morelli 2020) and afford a unique survival advantage compared to hares living in harsh matrix habitats of the western USA. Clearly, more study is warranted to understand these dynamics. A logical first step would be a range-wide examination of the influence of optimal and matrix habitat on snowshoe hare demography.

Our findings are readily generalized to populations of other species persisting near range limits. Populations along or near range limits often are exposed to variable climate and resource availability relative to core populations (Hampe and Petit 2005, Pironon et al. 2017). Our study of three different landscapes that are representative of hare habitat in the northeastern USA highlights how this variability can cause divergent population dynamics. It is plausible that much of the southeastern edge of hare range has similar dynamics to that of the WMNF. For instance, the disturbance regime of the forests in the WMNF have a long return interval and early-regenerating stands are patchily distributed within a matrix of high biomass forests (Sprugel 1976, Lorimer and White 2003); both of these factors likely contribute to stable and low hare densities. In a broader sense, these forest conditions are representative of the high biomass temperate and boreal forests of the northeastern USA (Fig. 1, top left panel). A low-density refuge provided by these forests may explain why some early successional species like hares persist in regions with marginal climate (e.g. Pennsylvania; Gigliotti 2016) or the recent expansion of moose to southern New England that are freed from high parasite loads when densities are low (Samuel 2007, Wattles and DeStefano 2011).

Our study has some limitations. First, despite sampling across a broad spatial gradient with numerous replicates for each stand type within each landscape, we relied on pellet surveys for indexing density and population fluctuations. This approach has drawbacks, especially for studies with low pellet counts that are not as predictive of absolute density (Mills et al. 2005). Ideally, future studies should evaluate annual population fluctuations using capture–recapture or similar methodologies that provide direct estimates of abundance or density (Cheng et al. 2017, Jensen et al. 2022). Next, our survival analysis had a relatively low sample size, especially for the WMNF. We attempted to mitigate errors that arise from this problem by only fitting a univariate model, as done previously (Gigliotti and Diefenbach 2018, Kumar et al. 2018). Finally, we did not have data on predator species richness and densities that matched the scale of our study. These data would have been useful for identifying the effects of the predator community on hare density and survival. Given these shortcomings, collecting demographic (e.g. reproduction, dispersal), genetic, and morphometric data and using integrated population models (Schaub and Abadi 2011), including data on predator populations, could allow an evaluation of the GEH and hypotheses related to life-history theory and population cycling.

Conclusion

Our study provides insight on how resource availability influences herbivore populations along trailing edges. In accordance with the GEH, the availability of habitat resources likely elicited a strong bottom-up effect that triggered density-dependent predation and parasitism; hares living in resource-limited environments had lower and relatively stable populations, yet higher survival, when compared to those living in resource-rich environments. Low-density hare populations living in resource-limited environments appear to have a survival advantage that may explain persistence of some populations along trailing edges, as predicted by the GEH. We hypothesize that the extent to which this dynamic occurs is conditional on the quality of matrix habitat and the presence of generalist predators. While there is more work to be done to evaluate the applicability of the GEH beyond hares in the northeastern USA, there is evidence that it applies to other species, including marine animals (Seitz et al. 2001, Griffen and Williamson 2008), insects (Choutt et al. 2011), and moose (Wattles and DeStefano 2011). In fact, lowering density via harvest has been recently used as a mitigating strategy to relieve trailing edge moose populations burdened by intense parasitism (Ellingwood et al. 2020). Provided that the range of a species is shaped by numerous drivers other than climate (Doak and Morris 2010), a more thorough assessment of biotic and demographic factors is needed to effectively conserve and manage populations along trailing edges.

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Author contributions

Alexej Sirén: Conceptualization (lead); Investigation (lead); Formal Analysis (lead); Data curation (lead); Funding acquisition (lead); Writing – original draft (lead); Writing – review and editing (lead). **Marketa Zimova**: Investigation (supporting); Writing – review and editing (supporting). **Chris S. Sutherland**: Formal Analysis (supporting); Writing – review and editing (supporting). **John T. Finn**: Formal Analysis (supporting); Writing – review and editing (supporting). **Jillian R. Kilborn**: Conceptualization (supporting); Investigation (supporting); Funding acquisition (supporting); Resources (lead); Writing – review and editing (supporting). **Rachel M. Cliché**: Conceptualization (supporting); Investigation (supporting); Funding acquisition (supporting); Resources (lead); Writing – review and editing (supporting). **Leighlan S. Prout**: Conceptualization (supporting); Investigation (supporting); Funding acquisition (supporting); Resources (lead); Writing – review and editing (supporting). **L. Scott Mills**: Writing – review and editing (supporting). **Toni Lyn Morelli**: Funding acquisition (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.r2280gbhw (Sirén et al. 2023).

Supporting information

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

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