

RESEARCH ARTICLE

Can internal range structure predict range shifts?

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Abstract

1. Poleward and uphill range shifts are a common—but variable—response to climate change. We lack understanding regarding this interspecific variation; for example, functional traits show weak or mixed ability to predict range shifts.
2. Characteristics of species' ranges may enhance prediction of range shifts. However, the explanatory power of many range characteristics—especially within-range abundance patterns—remains untested.
3. Here, we introduce a hypothesis framework for predicting range-limit population trends and range shifts from the internal structure of the geographic range, specifically range edge hardness, defined as abundance within range edges relative to the whole range. The inertia hypothesis predicts that high edge abundance facilitates expansions along the leading range edge but creates inertia (either more individuals must disperse or perish) at the trailing range edge such that the trailing edge recedes slowly. In contrast, the limitation hypothesis suggests that hard range edges are the signature of strong limits (e.g. biotic interactions) that force faster contraction of the trailing edge but block expansions at the leading edge of the range.
4. Using a long-term avian monitoring dataset from northern Minnesota, USA, we estimated population trends for 35 trailing-edge species and 18 leading-edge species and modelled their population trends as a function of range edge hardness derived from eBird data. We found limited evidence of associations between range edge hardness and range-limit population trends. Trailing-edge species with harder range edges were slightly more likely to be declining, demonstrating weak support for the limitation hypothesis. In contrast, leading-edge species with harder range edges were slightly more likely to be increasing, demonstrating weak support for the inertia hypothesis.
5. These opposing results for the leading and trailing range edges might suggest that different mechanisms underpin range expansions and contractions, respectively. As data and state-of-the-art modelling efforts continue to proliferate, we will be ever better equipped to map abundance patterns within species' ranges, offering opportunities to anticipate range shifts through the lens of the geographic range.

KEYWORDS

biogeography, climate change, macroecology, range shifts, species distributions

1 | INTRODUCTION

Anthropogenic climate change is changing the physiology, morphology, behaviour, phenology, and distributions of organisms (Chen et al., 2011; Cohen et al., 2018; Gardner et al., 2011; Huey et al., 2012; Jirinec et al., 2021; Sih, 2013; Youngflesh et al., 2022). Poleward and upslope range shifts represent one of the most frequently observed fingerprints of climate change (Chen et al., 2011; Freeman et al., 2018). And yet, we have a decidedly poor ability to understand and anticipate why certain species demonstrate range shifts and others do not, and why species shift their ranges with differing velocities (Beissinger & Riddell, 2021).

Species traits often demonstrate a weak or mixed ability to predict range shifts (Angert et al., 2011; Beissinger & Riddell, 2021; Brown et al., 2016; Comte et al., 2024; Estrada et al., 2016; MacLean & Beissinger, 2017; Santini et al., 2016). Of the traits that have been evaluated thus far, those associated with dispersal capacity (e.g. body size, natal dispersal distance) and ecological niche breadth (e.g. habitat breadth) seem to hold the most predictive power, with vagile habitat generalists most likely to show range shifts (MacLean & Beissinger, 2017; Pöyry et al., 2009). Characteristics of species' geographic ranges (so-called "externalities" by Beissinger & Riddell, 2021) may offer a better opportunity to explain range shifts and associated population trends at range limits. For example, the thermal niche of a species (computed by extracting the average temperature within a species' range map) is often associated with local population trends; in Europe, for instance, bird species associated with cooler temperatures are declining, while "warm" species are increasing (Jiguet et al., 2007, 2010). Range size—likely serving as a proxy for ecological niche breadth—has been positively correlated with range shifts (Lancaster, 2022; Yang et al., 2020). And finally, range position may explain range shifts, with higher-latitude species more likely to demonstrate range shifts than low-latitude species (Ramalho et al., 2023). However, associations between range shifts and other range characteristics—especially those relating to the within-range abundance variation, which we call internal range structure—remain unexplored (Brown et al., 1996; Gaston, 2003; Sexton et al., 2009).

Ranges are the geographic manifestations of species' niches, and thus range edges offer a laboratory of sorts for ecologists to explore the factors that define species' niches (Sexton et al., 2009). The niche has many dimensions, which can be broadly grouped into abiotic factors (e.g. climate), biotic factors (e.g. competing species), and dispersal factors (Naujokaitis-Lewis & Fortin, 2016; Shepard et al., 2021; Sirén & Morelli, 2020). This interplay of factors explains why the realised niche—expressed as a species' geographic range—is smaller than the fundamental niche, or the range a species could theoretically occupy given its physiological tolerances (typically to temperature; Brown et al., 1996; Gaston, 2003; Moore et al., 2023; Sexton et al., 2009). Moreover, this phenomenon of niche underfilling may explain why some species have not exhibited range shifts as the temperature warms; that is, a range shift may not occur if

warming does not exceed the fundamental thermal niche of a species experiencing range limitation from dispersal or biotic factors (Lawlor et al., 2024). Finally, the relative influence of abiotic, biotic, and dispersal factors may vary over space. For example, one of the classic ideas in biogeography is that abiotic factors more strongly limit the "cold", or high-latitude or elevation margin of a species' range, while biotic factors (e.g. competition) more strongly limit the "warm", or low-latitude or elevation, margin (Darwin, 1859; Moore et al., 2023; Paquette & Hargreaves, 2021; Schemske et al., 2009; Sirén & Morelli, 2020).

Patterns of abundance near the range edge may hint at the relative influence of factors defining a species' niche and thus the species' likelihood of shifting its range in response to climate change. On one end of the spectrum, abiotic gradients are expected to produce diffuse range boundaries, with lower abundances near the range margin and higher abundances towards the range core, because demographic rates such as survival and fecundity are expected to decline as conditions become less hospitable (Banks-Leite et al., 2022; Fristoe et al., 2023; Martin et al., 2024; Pironon et al., 2017). On the opposite side of the spectrum, dispersal barriers such as rivers, coastlines, or hostile landscapes may create an abrupt range edge such that high abundances are observed up to the edge of the range (Anderson et al., 2012; Banks-Leite et al., 2022). Between these extremes, biotic factors—such as competition with a sister taxon or specialisation on certain habitats—are expected to produce range edges with intermediate texture (Sirén & Morelli, 2020). Understanding the relative importance of these factors in limiting the distribution of a species may enhance predictive capacity of ongoing and future range shifts. However, we are not aware of any evaluations of the association between the internal structure of species' geographic ranges and range shifts.

Our objective was to investigate whether the internal structure of geographic ranges—here focusing on abundance at range limits relative to range-wide abundance, which we call *range edge hardness*—influences population trends near range limits. We considered two hypotheses, each of which implies opposing behaviours at the leading and trailing range margins and assumes that leading-edge populations should generally increase while trailing-edge populations should generally decrease (Figure 1). The *inertia hypothesis* suggests that high abundance at the range limit (i.e. a harder range edge) results in faster expansions at leading range edges and slower contractions at the trailing edge. At the leading edge, high abundance represents a larger pool of propagules to export beyond the range edge compared to a species with diffuse range edges (Melles et al., 2011). Conversely, high abundance near the trailing edge creates inertia: a larger number of individuals must disperse (or perish or fail to reproduce, if trailing-edge contraction is driven by changes in births and deaths rather than dispersal) for the range limit to shift in comparison to a species with a diffuse range limit. Thus, the inertia hypothesis predicts larger population changes for species with hard range edges near the leading edge of their range, and for species with soft range edges near the trailing edge of their range (Figure 1). The *limitation hypothesis* suggests that high abundance at

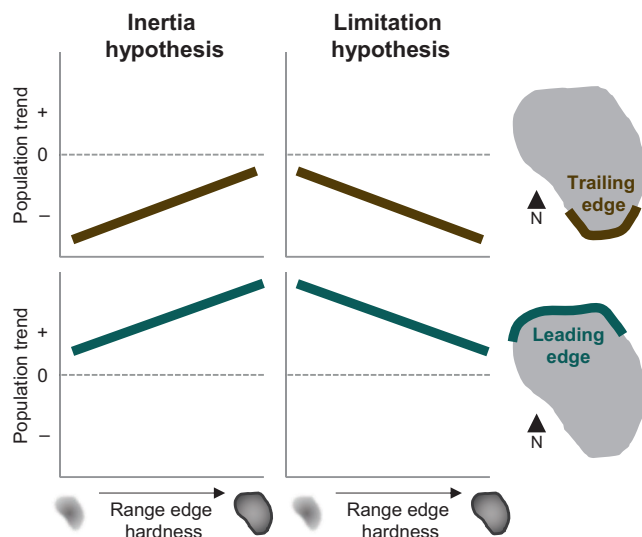


FIGURE 1 Relationships between population trend and range edge hardness (i.e. abundance within range edges relative to abundance across the whole range) predicted by the two hypotheses, for the trailing (top row; brown) and leading (bottom row; teal) edges of species' ranges.

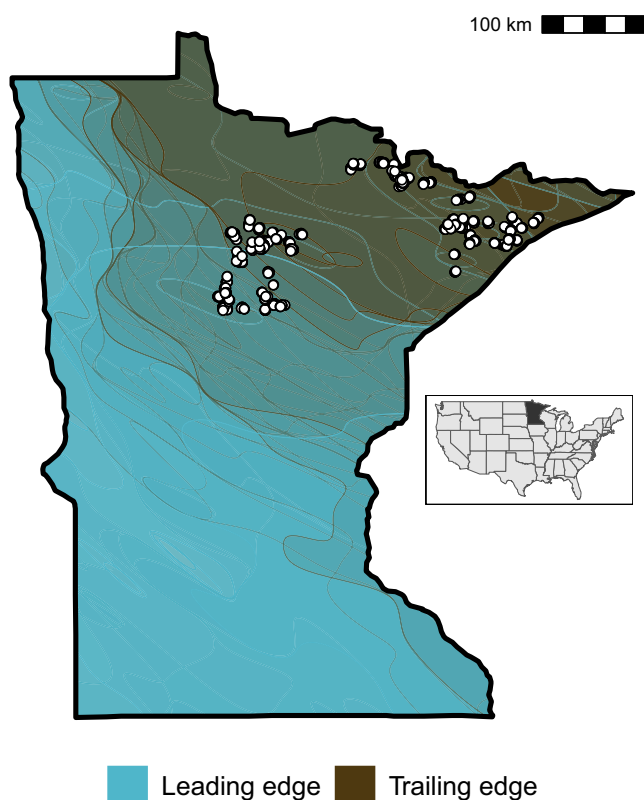


FIGURE 2 The state of Minnesota, USA, showing the sites (white points) at which bird surveys were conducted 1995–2023. The fill is layered range maps of the 53 focal species (brown: Trailing-edge species, $n=35$; teal: Leading-edge species, $n=18$). The inset shows the location of Minnesota within the continental United States.

the range limit is the signature of non-climatic niche limitations (e.g. competitors or habitat specialisation) which prevent or obfuscate a species' response to temperature changes. At the leading edge, such limitations may inhibit range expansions; for example, a species reliant on mature forest cannot expand beyond its range edge where this habitat does not occur—even if the thermal niche expands beyond the edge—until habitat develops in extralimital areas (Melles et al., 2011). On the other hand, if such limitations (e.g. a competitor species) encroach upon the trailing edge of a species' range, they may force the trailing edge to contract (again, either through dispersal of individuals or by affecting the number of births and deaths), even if the lost range area is ostensibly within the thermal niche of the species. Thus, the limitation hypothesis predicts smaller population changes for species with soft range edges near the trailing edge of their range, and for species with hard range edges near the leading edge of their range (Figure 1). In summary, the inertia hypothesis assumes that species are “free” to track changing temperatures and that abundance patterns influence the velocity of range shifts, whereas the limitation hypothesis assumes that non-climatic factors eclipse the importance of climate factors and that abundance patterns provide evidence for the influence of these non-climatic factors.

We address these objectives using 29 years of data from a standardised breeding bird monitoring program in northern Minnesota, USA, a region where many species reach their range limits (Figure 2) and where several taiga species have been declining and several southern species (often associated with deciduous and mixed forests) have been increasing (Grinde et al., 2017, 2023). We estimated population trends for 53 bird species (35 trailing-edge species, 18 leading-edge species) and modelled these trend estimates as a function of range edge hardness metrics derived from range-wide abundance maps produced by eBird (Fink et al., 2022).

2 | METHODS

2.1 | Point count surveys

We conducted standardised avian point counts at 1044 points within 356 forest stands in the Superior and Chippewa National Forests in northern Minnesota from 1995 to 2023 (Figure 2). The study region falls within the Laurentian Mixed Forest Province, a transitional zone between deciduous forest (dominated by taxa such as maples *Acer* and oaks *Quercus*) to the south and boreal forest (dominated by coniferous taxa *Pinus*, *Picea* and *Larix*) to the north (Kilgore et al., 2005). Within the study region, there is variation such that sites farther to the south and west (Chippewa National Forest) are drier and have more pines (*Pinus*), maples (*Acer*) and oaks (*Quercus*), whereas sites farther to the east and north (Superior National Forest) are wetter and have more spruces (*Picea*), aspens (*Populus*) and birch (*Betula*; Kilgore et al., 2005). Many bird species reach their range limits in

the region, and the east–west, as well as north–south orientation of these range limits (Figure 2) reflect these broad patterns of forest composition.

At the onset of the project, 356 forest stands were selected following a stratified random design by dominant tree species and stocking density. Permission was not required to conduct the fieldwork. For each national forest, we selected a set of stands (minimum area: 16 ha) from each stratum such that the proportion of stands of each category was equal to the proportion of that stand category within each national forest. Within each stand, we established three point count locations such that points were spaced by at least 220 m and at least 100 m from the edge of the forest stand (Etterson et al., 2009). In a few cases, only one (nine stands) or two (eight stands) points were established within stands that were too small to accommodate three points, and in two cases, four points were established in large stands. The total number of points was 1044. Trained observers conducted 10-min point counts during the breeding season (1 June–14 July) in the morning (starting no earlier than 30 min before sunrise and no later than 4 h after sunrise) on days with little wind ($<15 \text{ km h}^{-1}$) and little or no precipitation. Observers recorded all species and estimated distances to detected birds (0–25 m, 25–50 m, 50–100 m, or >100 m). We filtered the dataset to retain individuals detected within 100 m, omit flyovers, and omit species with <10 observations or those not well-sampled with the point count methodology (e.g. waterbirds and nocturnal species). This left us with 96 species. Finally, to select focal leading- and trailing-edge species, we calculated the distance between each point count site and each species' range edge (see details below) and retained species that had a range edge within 100 km of any of the point count sites, leaving us with 35 trailing-edge species and 18 leading-edge species.

2.2 | Calculating range edge hardness

We calculated the hardness of species' range edges using published abundance maps from eBird and climate maps from WorldClim (Figure 2). On 26 April 2023, we downloaded breeding-season relative abundance maps (26.7×26.7 km resolution) for all the species from the eBird Status and Trends data product (Fink et al., 2022) using the *ebirdst* R package (Strimas-Mackey et al., 2022). These data products are derived from eBird, a global community science initiative in which birdwatchers submit checklists of birds they observe; the data are semi-structured, meaning that metadata such as time-of-day and distance travelled are collected but locations are not sampled randomly (Sullivan et al., 2009). The Status and Trends products are the output of machine-learning models leveraged to the data following stringent data filtering rules based on observation metadata (Fink et al., 2010; Johnston et al., 2022). The estimated relative abundance is interpreted as the expected number of birds reported by an experienced birdwatcher on a 1-km checklist during the morning under optimal weather conditions (Fink et al., 2010).

We reprojected and resampled the relative abundance maps to match the 10-min spatial resolution WorldClim data product (Fick & Hijmans, 2017). We extracted the mean temperature of the warmest quarter (i.e. the breeding season) from all cells where relative abundance was greater than zero (Figure 3a). We then defined the leading and trailing range edges as the 10% coldest and warmest cells, respectively, within the distribution of the species (Figure 3a). We calculated the hardness of each range edge as the average abundance within the edge divided by the average abundance across the species' entire range. Thus, the range hardness metric quantifies abundance in the range edge relative to overall range (Figure 3). For reference, values of 1.00 represent a species' range for which abundance at the range edges equals abundance across the entire range, while values approaching zero indicate very diffuse range edges (Figure 3b). In addition, we calculated species temperature index as the range-wide average of the mean temperature of the warmest quarter to be included in models, since past research indicates this value is associated with population trends of species (Jiguet et al., 2007, 2010).

2.3 | Modelling approach

We used a two-stage approach in which we first estimated population trends for the 53 edge species (Figure 2) with a Bayesian hierarchical multispecies model and then used separate models to relate the population trends of the 35 trailing-edge and 18 leading-edge species to edge hardness metrics to test our hypotheses.

2.3.1 | Step 1: Estimate population trends

The first model—used with the counts produced by the Minnesota point counts—was a generalised linear mixed-effect model with a Poisson response:

$$y_i \sim \text{Poisson}(\lambda_i),$$

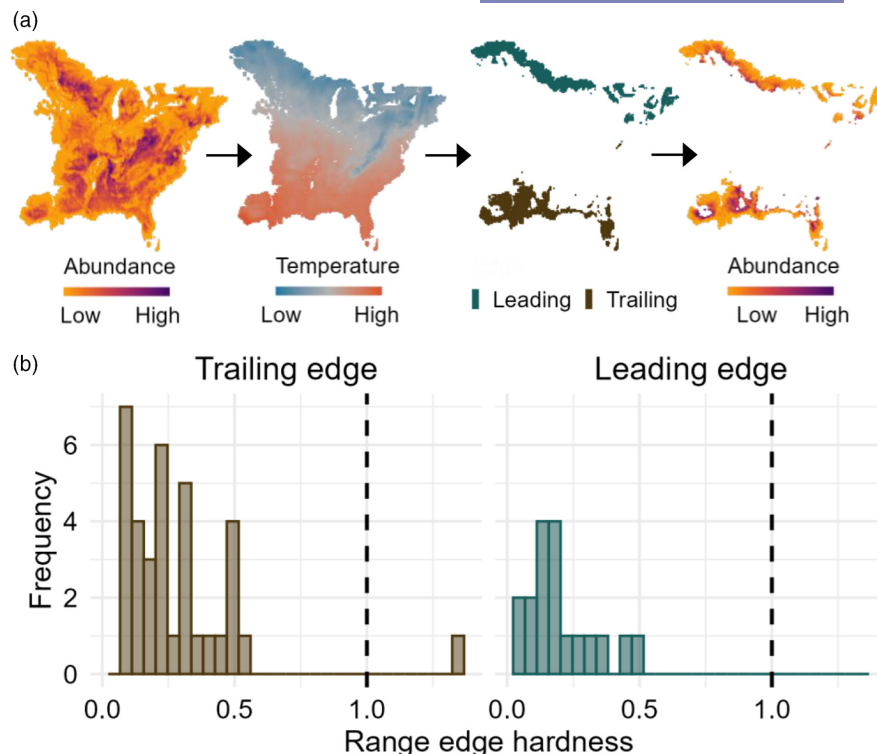
where y_i is the count for observation i (i.e. a location–species–year combination). We modelled the expected count λ_i with a log-linear regression with a year covariate YEAR_i to estimate population trends, survey covariates day-of-year DOY_i and time-of-day TIME_i , and a random-effects structure to account for variation in counts by species, among stands, and by observer:

$$\log(\lambda_i) = \beta_{1,\text{SP}[i]} + \beta_{2,\text{SP}[i]}\text{YEAR}_i + \beta_{3,\text{SP}[i]}\text{DOY}_i + \beta_{4,\text{SP}[i]}\text{TIME}_i + \epsilon_{\text{SP,STAND}[i]} + \kappa_{\text{OBS}[i]},$$

where $\beta_{1,\text{SP}[i]}$ is the intercept, $\beta_{2,\text{SP}[i]}$ is the population trend (our target of inference), $\beta_{3,\text{SP}[i]}$ is the effect of day-of-year, and $\beta_{4,\text{SP}[i]}$ is the effect of time-of-day. These parameters vary by species (notice the $\text{SP}[i]$ indices) and are modelled hierarchically; for example, the intercept β_1 for species $s = 1, 2, 3, \dots, S$ is modelled as a draw from a normal distribution:

$$\beta_{1,s} \sim \text{Normal}(\mu_{\beta_1}, \sigma_{\beta_1}),$$

FIGURE 3 (a) Process for deriving range hardness based on abundance and temperature. The eBird Status & Trends breeding-season abundance map for each species (Yellow-throated Vireo, *Vireo flavifrons* shown) is overlaid with a map of temperature of the warmest quarter, and the leading and trailing range edges are defined as the 10% coldest and warmest cells within the species' range, respectively. Range edge hardness is the average abundance within each edge divided by average abundance across the whole range. (b) Distribution of range edge hardness values for the trailing-edge ($n=35$) and leading-edge ($n=18$) species analysed. The dashed vertical line represents a range for which edge abundance equals abundance across the whole range. Thus, most species show much lower abundance within range edges than across the whole range.



where μ_{β_1} is the average intercept across species and σ_{β_1} is the standard deviation among species-level intercepts. Returning the equation for the expected count, $\varepsilon_{SP,STAND[j]}$ adjusts the intercept for each species-stand combination; for example, the effect for species-stand combination $j=1, 2, 3, \dots, J$ is modelled as:

$$\varepsilon_j \sim \text{Normal}(0, \sigma_\varepsilon).$$

Finally, $\kappa_{OBS[j]}$ adjusts the intercept based on the observer who conducted the survey; the adjustment for observer $k=1, 2, 3, \dots, K$ is modelled as:

$$\kappa_k \sim \text{Normal}(0, \sigma_\kappa).$$

We fit the model using the brms (Bürkner, 2017) interface to cmdstan (Carpenter et al., 2017) in an R environment (R Core Team, 2023) using four Markov Chain Monte Carlo chains each run for 5000 iterations and discarding the initial 3000 as warm-up. To ensure convergence, we checked that the convergence diagnostic $\hat{R} < 1.1$ (Brooks & Gelman, 1998; Vehtari et al., 2021).

2.3.2 | Step 2: Relate population trends to range edge hardness

The second step was a linear regression in which the response variable—population trend $\beta_{1,s}$ (estimated in the first modelling step) for the 35 trailing-edge and 18 leading-edge species—was modelled as a draw from a normal distribution with mean μ_s and standard deviation σ :

$$\beta_{1,s} \sim \text{Normal}(\mu_s, \sigma).$$

We modelled the expected value as a function of predictor variables edge hardness h_s (log transformed), species temperature index t_s , and their interaction:

$$\mu_s = \gamma_1 + \gamma_2 \log(h_s) + \gamma_3 t_s + \gamma_4 t_s \log(h_s),$$

where γ_1 is the intercept, γ_2 is the coefficient of edge hardness, γ_3 is the coefficient of species temperature index, and γ_4 is the coefficient for the interaction. We fit separate models for the leading- and trailing-edge species. In addition, we repeated the secondary analysis for trailing-edge species with one species with an extreme edge hardness value omitted. We ran each model 1000 times, each with a different posterior sample of $\beta_{1,s}$ from Step 1 to propagate the uncertainty in the estimates of species population trends (Behney, 2020; Gilbert et al., 2023). We fit models in the brms (Bürkner, 2017) interface to Rstan (Carpenter et al., 2017) in an R environment (Gilbert, 2024; R Core Team, 2023).

3 | RESULTS

3.1 | Trailing edge species

Of the 35 trailing-edge species, the mean range edge hardness was 0.29 and the standard deviation was 0.23 (Figure 3b). Thus, for most species, abundance in the trailing range edge was approximately a quarter of the magnitude of the average abundance across the species' entire range (Figure 3b). One species (Connecticut Warbler, *Oporornis agilis*) had a range hardness metric >1.00 , indicating that its average abundance in the trailing edge of its range was higher than the average range-wide abundance (Figure 3b).

Eight species (22.9%) showed increasing population trends while nine species (25.7%) showed decreasing population trends (based on 95% credible intervals not including 0); the remaining 18 species (28.6%) showed no clear trends (Figures S1 and S2).

Species with harder trailing range edges were slightly more likely to show decreasing population trends (Figure 4). The effect of range edge hardness was estimated to be -0.09 [68% CI: -0.15 , -0.03 ; 95% CI: -0.21 , 0.03] (Figure 5). Species temperature index showed a comparatively weaker association with population trends (Figure 5); its main effect was estimated to be -0.04 [68% CI: -0.10 , 0.02 ; 95% CI: -0.16 , 0.08], and its interaction with range edge hardness was estimated as -0.01 [68% CI: -0.07 , 0.04 ; 95% CI: -0.13 , 0.10]. However, when Connecticut Warbler—a high-leverage species due to its anomalously high edge hardness value—was omitted from the secondary analysis, the negative relationship between range edge hardness and

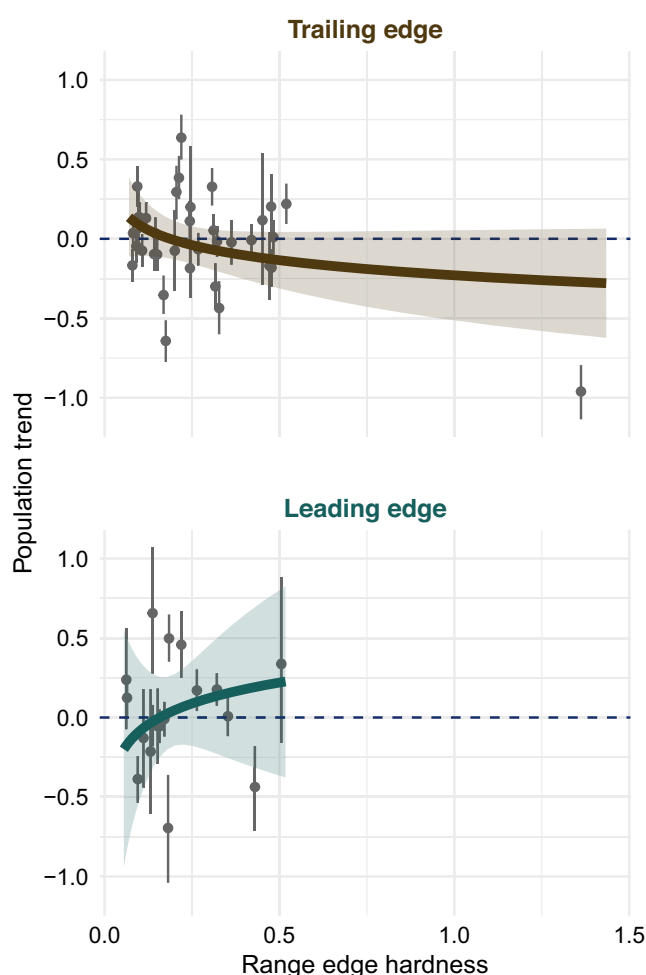


FIGURE 4 Predicted relationship between species' population trends and range edge hardness for trailing-edge species (top) and leading-edge species (bottom). Points and vertical bars and posterior means and 95% credible intervals for population trend estimates. Coloured lines and shaded regions are the mean and 95% credible interval for the predicted relationship between range edge hardness and population trend. See Figure S3 for an alternative version of this plot for which Connecticut Warbler (the extreme value in the top panel) was omitted.

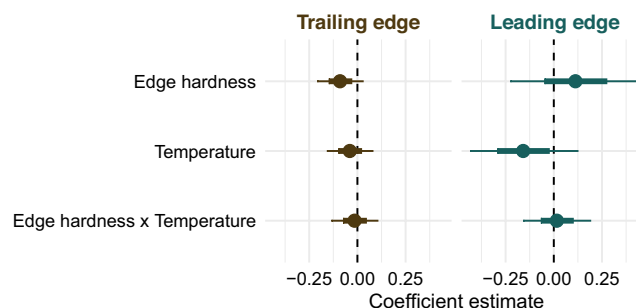


FIGURE 5 Coefficient estimates for secondary analysis in which species' population trend (response variable) was modelled as a function of range edge hardness (mean abundance in range edge divided by mean abundance across the whole range), species temperature index (average temperature across species range), and the interaction of these two variables. Models were run separately for trailing-edge (left) and leading-edge (right) species. Points are posterior means, thick horizontal bars are 68% credible intervals, and thin horizontal bars are 95% credible intervals. See Figure S4 for an alternative version of this plot for which Connecticut Warbler (the extreme value in the top panel) was omitted.

population trend disappeared (Figures S3 and S4). This suggests that the original result (Figure 4) should be interpreted cautiously and that is perhaps better to conclude that there is no association between trailing-edge range edge hardness and population trend.

3.2 | Leading edge species

Of the 18 leading-edge species, the mean range edge hardness was 0.20 and the standard deviation was 0.12 (Figure 3b). Six species (33.3%) showed increasing population trends while three species (16.7%) showed decreasing population trends (based on 95% credible intervals); the remaining nine species (50%) showed no clear trends (Figures S1 and S2).

Species with harder leading edges of their range were slightly more likely to show increasing population trends (Figure 4). The effect of range edge hardness was estimated as 0.11 [68% CI: -0.05 , 0.27 ; 95% CI: -0.23 , 0.44]; note that both the 68% and 95% credible intervals overlap zero (Figure 5). In contrast to the trailing-edge analysis, species temperature index showed an association with population trends, with "warmer" (i.e. more southerly distributed) species more likely to show decreasing trends (Figure 5); the effect was estimated as -0.16 [68% CI -0.29 , -0.03 ; 95% CI -0.43 , 0.12]. However, there was limited evidence of an interaction between species temperature index and range edge hardness (Figure 5); the interaction coefficient was estimated as 0.02 [68% CI: -0.07 , 0.10 ; 95% CI: -0.16 , 0.19].

4 | DISCUSSION

We introduced a novel hypothesis framework that predicts relationships between range shifts and internal range structure; however,

our empirical application found limited evidence of associations between range edge hardness and range-limit population trends. Though associations were weak, trailing-edge and leading-edge species showed opposing relationships with range edge hardness: trailing-edge species with harder range edges were slightly more likely to show decreasing population trends (only if a high-leverage species was included), while leading-edge species with harder range edges were slightly more likely to show increasing population trends (Figure 4). Thus, the trailing-edge species weakly supported the limitation hypothesis, which predicts a negative relationship between range-limit population trends and range edge hardness (Figure 1). In contrast, the leading-edge species weakly supported the inertia hypothesis, which predicts a positive relationship between range-limit population trends and range edge hardness (Figure 1). These contrasting results may indicate that abundance patterns reflect differing processes at the leading versus trailing edges of species' ranges.

The limitation hypothesis suggests that hard range edges are the result of non-climatic factors, including biotic interactions such as competition or specialisation on certain resources. For trailing-edge species, there are several prospective biotic interactions that may form hard range edges and, when perturbed, might cause rapid population declines at range limits. For example, the presence of a competitor (e.g., a sister species or one fulfilling a similar ecological niche) may limit the trailing edge of a species' distribution (Paquette & Hargreaves, 2021), and if that competitor shifts its range poleward, it may "push" the other species ahead of it. For example, the contact zone between the Black-capped Chickadee (*Poecile atricapillus*) and its more southerly distributed sister species, the Carolina Chickadee (*P. carolinensis*), is shifting northward by approximately 1.6 km per decade (Driver et al., 2022; Taylor et al., 2014). Cold winter temperatures define the northern limit of the Carolina Chickadee's distribution, and the species has been expanding northward as the climate warms (Driver et al., 2022; Olson et al., 2010). Moreover, the Carolina Chickadee dominates in interspecific interactions, and female Black-capped Chickadees prefer to pair with male Carolina Chickadees, producing less-fit hybrids (Bronson et al., 2003; Driver et al., 2022; Reudink et al., 2006). Thus, the retreat of the Black-capped Chickadee's trailing range edge is formed through a climate-mediated interaction with a sister species on both whole-organism and genomic levels (Taylor et al., 2014). Alternatively, a hard trailing edge may form through reliance on a particular resource, such as specific vegetation community or an insect taxon used to feed young. If such a system experiences disruption from climate change—for example, if habitat regeneration fails following altered disturbance intervals or if phenological mismatch arises between caterpillar emergence and nesting—the trailing-edge species may experience rapid declines (Baltzer et al., 2021; Both et al., 2006; Møller et al., 2008; Simmonds et al., 2020).

Leading-edge species showed weak support for the inertia hypothesis, which, for leading range edges, suggests that hard range edges represent a large pool of prospective emigrants to export beyond the range limit. If animals disperse randomly—for example, performing a random walk—abundance at the range limit should show

a positive relationship to both the number of individuals moving beyond the range limit and the maximum distance moved. This would increase the chance of these dispersing individuals establishing populations beyond the range limit, thus driving a range shift. Of course, birds, unlike some plants, do not often show random dispersal patterns (Hubbell, 2005); instead, factors such as resource availability and the presence of con- or heterospecifics influence dispersal decisions (Bowler & Benton, 2005). Many species may show positive density-dependent dispersal by which emigration rates and/or distances dispersed are higher from areas with greater population density (Bowler & Benton, 2005; Matthysen, 2005). If this is the case, species with hard range edges may be more likely to have individuals disperse beyond the range limit. However, theoretical modelling suggests that subsequent range shifts are slower for species with positive density-dependent dispersal, since newly colonised locations must be "filled up" to high densities before individuals disperse to additional extralimital areas (Altwegg et al., 2013).

The zeitgeist of climate change ecology is that species are expanding their ranges poleward or upward in elevation to track their thermal niches as the climate warms (Chen et al., 2011; Freeman et al., 2018; Langham et al., 2015; Parmesan, 2006). Under this paradigm, we would expect that trailing-edge species in our system—primarily those associated with taiga or boreal landscapes—would decline as leading-edge species (associated with deciduous or mixed forest) increase (Figure 1). This expectation did not manifest in our system; similar numbers of species showed population increases and decreases, respectively, within the two range-edge categories (Figures S1 and S2); for example, 22.9% of the trailing-edge species showed *increasing* population trends, while only 25.7% showed the expected decreasing population trends (Figure S1; Table S1). Auxiliary analyses indicated only limited evidence that phylogenetic dependence influenced these patterns (Figure S5; Table S2). These findings hint at more complex processes affecting the distributions of species near their range limits (DeLuca & King, 2017; Freeman et al., 2022; Grenouillet & Comte, 2014; Siefertman et al., 2023; Tagliari et al., 2021). For example, several trailing-edge warbler species with increasing population trends (e.g. Tennessee Warbler *Leiothlypis peregrina* and Cape May Warbler *Setophaga tigrina*) are known to benefit from outbreaks of spruce budworm *Choristoneura fumiferana* (Drever et al., 2018; Moisan Perrier et al., 2021), which has shown persistent outbreaks in northern Minnesota in recent decades (MDNR, 2021; Patton et al., 2019). Thus, local-scale biotic interactions (e.g. prevalence of a prey species), habitat amount, or habitat connectivity may override broad-scale climate trends in governing the population trends of species at the limits of their distributions (Caro et al., 2022; Haight et al., 2023; Hodgson et al., 2022).

How broadly applicable is our hypothesis framework (Figure 1) for associating range edge hardness to range limit population trends and range shifts? We developed the framework with reference to vagile terrestrial vertebrates (birds) in a non-mountainous region. In theory, the framework should apply to elevational range shifts as well as latitudinal ones, with the caveat that abiotic conditions change over shorter spatial distances in mountains, meaning that

range shifts may be less perceptible there (Pinsky et al., 2022) and require more precise spatial measurement (Freeman et al., 2018). Beyond terrestrial systems, marine environments may be ideal for further evaluating the framework because marine species show larger and faster range shifts than terrestrial species, likely because marine environments provide less opportunity for in-situ adaptation strategies such as behavioural thermoregulation because there is less microclimate variability in oceans than on land (Lenoir et al., 2020; Pinsky et al., 2019). In contrast, freshwater species often face hard barriers to dispersal (e.g. riverine network structure or anthropogenic barriers such as dams) and consequently may not follow the predictions described by our hypothesis framework (Graf, 1999; Pinsky et al., 2022).

Anthropogenic climate change has already driven changes in the distributions, behaviours, and traits of species (Beever et al., 2017; Chen et al., 2011; Gardner et al., 2011). We can expect further—and increasingly dramatic—effects of climate change on biodiversity within the short time horizons of our lives and those of our children (IPBES, 2019). Historically, we have suffered from limited ability to understand and anticipate whether or not species will shift their ranges in response to climate warming, and with what velocity (Beissinger & Riddell, 2021; Estrada et al., 2016; Lenoir & Svenning, 2015). We propose a new framework for understanding population trends at range limits and range shifts through the lens of the geographic range (Brown et al., 1996). This framework is timely because ecology is entering a data-rich era in which more types of data are accumulating at ever-increasing volumes (Farley et al., 2018; Hampton et al., 2013); meanwhile, new models are being developed for such data (Fink et al., 2023), allowing us to move beyond analyses based on binary range maps to ask how range-wide abundance patterns relate to range shifts. By better characterising patterns of abundance across species ranges, we may be better equipped to understand and predict species' range shifts (Beissinger & Riddell, 2021).

AUTHOR CONTRIBUTIONS

Neil A. Gilbert, Stephen R. Kolbe, and Alexis R. Grinde conceived the research. Neil A. Gilbert and Harold N. Eyster analysed the data. Neil A. Gilbert wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code are available on Zenodo <https://doi.org/10.5281/zenodo.13313906> (Gilbert, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Species included in the analysis.

Table S2. Mean (across 100 subsets of the dataset) of the estimated standard deviations for random terms from phylogenetic generalized linear mixed-effects models.

Figure S1. Estimated population trends for the 18 leading-edge (top panel) and 35 trailing-edge species (bottom panel) in northern Minnesota, USA.

Figure S2. Comparison of population trends (posterior mean) for leading-edge (teal; left) and trailing-edge (brown; right) species.

Figure S3. Relationships between range edge hardness and population trends as estimated in an additional analysis in which one trailing-edge species with a high value for edge hardness (Connecticut Warbler) was omitted.

Figure S4. Coefficient estimates for an additional analysis in which one trailing-edge species with a high value for edge hardness (Connecticut Warbler) was omitted.

Figure S5. Posterior means of trend coefficients plotted on the phylogeny of the 53 focal species.

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