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Warm-adapted encroachment outpaces cool-adapted retreat in a hotspot of trailing-edge population diversity in the southern Appalachian Mountains, USA

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ABSTRACT

Many populations near receding low-latitude range: margins are declining in response to climate change, but most studies of trailing-edge populations have focused on single species. Using 10 years (2014–2023) of avian survey data from a high-elevation trailing-edge population hotspot in the Appalachian Mountains, USA, we tested the hypothesis that high-elevation communities would experience turnover through thermophilization, as warm-adapted species near the center of their geographic ranges expand into regions formerly dominated by peripheral populations of cool-adapted species. Three of the nine cool-adapted, peripheral populations decreased in abundance, and whereas 6 species exhibited little change. For warm-adapted populations near the core of their range, 1 of 16 decreased in abundance, 11 increased, and 4 exhibited no change. Within the most abundant species in this community, our results indicate that warm-adapted species are expanding their ranges faster than the rate at which ranges of cool-adapted species are contracting. Avoiding future community turnover may require conservation strategies that maintain microclimates for cool-adapted species facing novel abiotic and biotic conditions at high elevations.

Keywords: abundance, Appalachian Mountains, community dynamics, climate change, elevational gradient, N-mixture, spatio-temporal dynamics, trailing-edge

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LAY SUMMARY

- Many populations of cool-adapted species at the edge of their geographic ranges are declining in response to climate change. At the same time, warm-adapted species are expanding their ranges as temperatures increase.
- We tested the hypothesis that high-elevation communities would experience greater change in species composition than lower elevation communities, and become increasingly dominated by warm-adapted species.
- Within the most abundant species in the community, several peripheral populations declined, whereas the majority of core populations increased or remained stable. The proportion of low elevation sites occupied by rear-edge populations also declined.
- Our study suggests that abundant, warm-adapted species are expanding their ranges faster than the rate at which cool-adapted species are contracting. Forest managers should maintain closed canopy forests and dense understory vegetation on north facing slopes to conserve cool-adapted species near the southern edge of their breeding range.
- Future research should determine if declines are the result of dispersal or decreasing fitness under changing climate conditions.

El avance de las especies adaptadas al calor supera el retroceso de las adaptadas al frío en el borde de un punto crítico de diversidad poblacional en el sur de las montañas Apalaches, EEUU

RESUMEN

Muchas poblaciones cercanas a los márgenes de rango en retroceso en latitudes bajas están disminuyendo en respuesta al cambio climático, pero la mayoría de los estudios sobre poblaciones en el borde de salida se han centrado en especies individuales. Utilizando 10 años (2014-2023) de datos de censos de aves del borde de salida de un punto crítico poblacional en elevaciones altas en las montañas Apalaches, EEUU, evaluamos la hipótesis de que las comunidades de alta elevación experimentarían un cambio a través de la termofilización, ya que las especies adaptadas al calor cercanas al centro de sus rangos geográficos se expanden hacia regiones anteriormente dominadas por poblaciones periféricas de especies adaptadas al frío. Tres de las 9 poblaciones periféricas adaptadas al frío disminuyeron en abundancia, mientras que 6 especies mostraron pocos cambios. En el caso de las poblaciones adaptadas al calor cercanas al núcleo de su rango, 1 de 16 disminuyó en

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abundancia, 11 aumentaron y 4 no mostraron cambios. Entre las especies más abundantes en esta comunidad, nuestros resultados indican que las especies adaptadas al calor están expandiendo sus rangos más rápidamente que el ritmo al que se están contrayendo los rangos de las especies adaptadas al frío. Evitar un recambio comunitario futuro podría requerir estrategias de conservación que mantengan microclimas para las especies adaptadas al frío que enfrentan nuevas condiciones abióticas y bióticas en elevaciones altas.

Palabras clave: abundancia, borde de salida, cambio climático, dinámicas comunitarias, dinámicas espacio-temporales, gradiente de elevación, mezcla-N, montañas Apalaches

INTRODUCTION

Population-level extinction risk from climate change is predicted to be highest at low-latitude range: margins (Hampe and Petit 2005, Sekercioğlu et al. 2008, Rushing et al. 2020, Stevens et al. 2023), where species frequently occur near their upper thermal tolerances and experience increased competition and predation pressure from warm-adapted species encroachment (MacArthur 1984, McDonald et al. 2012, Sunday et al. 2012, Akesson et al. 2021). Trailing-edge populations, defined as populations near the receding low-latitude margins of species' distribution ranges (Hampe and Petit 2005), are often genetically distinct from populations at the core of their range: and can be important components of regional biodiversity (Gaston 2009, Rehm et al. 2015, Ferrari et al. 2018, Merker and Chandler 2020). However, most research on trailing-edge populations, and peripheral populations in general has involved single-species studies, making it difficult to assess community-level consequences of population declines.

Community structure in regions with large proportions of trailing-edge species could be impacted by climate change in numerous ways. If cool-adapted species at the edge of their range: decline precipitously as warm-adapted populations encroach, complete community turnover could be possible through a process known as thermophilization (Hampe and Petit 2005, Sunday et al. 2012, Khaliq et al. 2024). Alternatively, if invasion by warm-adapted species happens faster than the retreat of cool-adapted trailing-edge species, rising temperatures could lead to increased species richness, even as trailing-edge populations decline (Lemoine and Böhning-Gaese 2003, La Sorte et al. 2009, Davey et al. 2012). Under this scenario, species richness might increase, but species composition will be greatly altered.

The speed of community encroachment by warm-adapted species, and the rate of decline of cool-adapted species, may depend on species-level traits other than thermal tolerance (Neate-Clegg et al. 2024). For instance, the ranges of short-lived species often shift upwards in elevation faster under climate change than long-lived species (Couet et al. 2022). In avian communities, long-distance neotropical migrants shift their cold-edge range: boundaries slower than short-distance migrants or resident species (Välimäki et al. 2016, Rushing et al. 2020, Stevens et al. 2023). Many migratory species have a slower phenological response to ongoing climate warming than resident species, which may translate to a reduced competitive advantage on the breeding grounds (Wittwer et al. 2015, MacLean and Beissinger, 2017). Thus, extinction risk may be higher for cool-adapted populations of migratory species than resident species, especially at low-latitude range: margins.

We used 10 years of avian survey data from a hotspot of trailing-edge population diversity (Merker and Chandler 2020) in the southern Appalachian Mountains to assess the generality of peripheral population declines near southern boundaries of breeding ranges and their consequences for community structure. We predicted species-specific shifts in abundance and occupancy would depend on range-position (peripheral vs. core), migratory strategy, and climate niche breadth. We predicted that cool-adapted, peripheral populations would decrease in abundance, and become increasingly restricted to high elevations. In contrast, we predicted that warm-adapted species near the center of their geographic ranges would increase in abundance and expand their distributions upwards in elevation. We further predicted long-distance migratory species would have slower rates of local range: shifts than short-distance migrants or residents.

METHODS

Study Area

The Nantahala National Forest in the southern Appalachian Mountains contains a high diversity of species at the trailing-edge of their breeding range: (Merker and Chandler 2020). Elevation within the region ranges from 660 to 1,590 m (Figure 1), with drier conditions found on the steeper, more exposed slopes in the eastern portion of the study area. High-elevation sites are cooler than those at lower elevations, with an average May temperature of 10.5°C above 1,300 m, compared to 14°C at 700 m. During the breeding season (May–July), sites above 1,300 m receive an average 26.4 cm of precipitation in comparison to only 18.2 cm of precipitation at the lowest elevations in the study area (Miniat et al. 2022).

Dominant and subdominant tree species include oaks (*Quercus* spp.), hickory (*Carya* spp.), yellow poplar (*Liriodendron tulipifera*), fraser magnolia (*Magnolia fraseri*), and common buckeye (*Aesculus flava*). Serviceberry (*Amelanchier* spp.) and witchhazel (*Hamamelis virginiana*) are common in the mid-story. Above 1,200 m elevation, the forest transitions to northern hardwood forests, dominated by black birch (*Betula lutea*), maple (*Acer* spp.), and northern red oak (*Quercus rubra*) (Hwang et al. 2014). Following declines of American chestnut (*Castanea dentata*) and Eastern hemlock (Tsuga canadensis), rhododendron (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), and huckleberry (*Vaccinium* spp. and *Gaylussacia* spp.) have become more common in the understory and in forest gaps (Elliott and Swank 2008).

Environmental Data

We calculated total annual precipitation for each year (2013–2022) based on 9 USDA Forest Service (USFS) climate stations (Miniat et al. 2022), and we used interpolations of PRISM data (Daly et al. 2008) to create smoothed precipitation layers spanning the study area. Temperature data were collected hourly from 34 temperature loggers (Onset Computer Corp., Bourne, MA, model number UA-002-64) distributed throughout the study area, as well as at 5 US Forest Service (USFS) climate stations (Miniat et al. 2022). Mean temperature in May 2014–2022 ranged from 0.43 to 33.6°C, with a mean annual precipitation of 230.6 cm. To

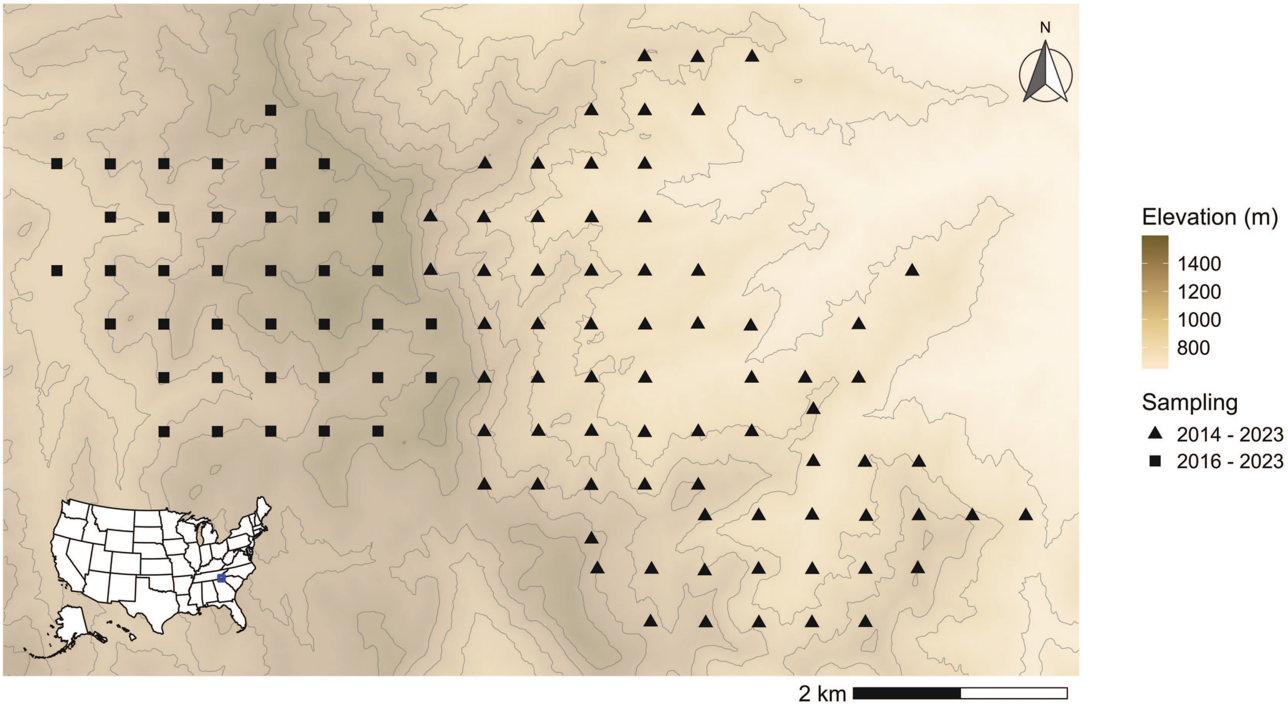

FIGURE 1. Map of point-count locations in the Nantahala National Forest, North Carolina, USA. Points shown as triangles (right side) were surveyed from 2014 to 2023. Locations shown as squares (left side) were surveyed starting in 2016.

represent the heat accumulation during the breeding season, we used growing degree-days, calculated as the monthly sum of the daily average number of degrees above 4°C (Lany et al. 2016, Cesaraccio et al. 2001). For many species in the southern Appalachian Mountains, May represents a critical part of the breeding season when birds build nests and begin provisioning fledglings (Lumpkin and Pearson 2013, Lewis et al. 2022). Therefore, we represented yearly temperature as the growing degree-days in May of each year (2013–2022).

Soil moisture and stream density in the study area follow an east-west gradient, with eastern slopes receiving and retaining less moisture. To account for the east-west gradient of soil moisture in the study area, we included the standardized easting coordinate of the site as a proxy for watershed moisture.

Surveys

Point-count surveys were conducted by trained technicians from 2014 to 2023. Seventy-one points were surveyed in 2014 and 2015, with 38 additional locations added in 2016 and surveyed each year thereafter. Each location was surveyed once per year during the breeding season (May to July). All surveys were conducted between sunrise and 5 hr after sunrise. Observers recorded the distance of all singing birds heard in a 10-min session split into 4 consecutive 2.5-min intervals. Observers also recorded noise level, wind, precipitation, and starting time for each survey.

Process Model

We analyzed point-count data using dynamic multi-species N-mixture models (Alldredge et al. 2007, Dail and Madsen 2011, Amundson et al. 2014). These models allow for the assessment of environmental effects on spatial and temporal variation in population growth rates while accounting for demographic stochasticity, serial correlation, and observation error arising from variation in detection probability. We categorized each species by migratory strategy (resident, short-distant migrant, or long-distance migrant) and range: position (rear-edge or core) to assess the effects of species traits on population trends. Following Merker and Chandler (2020), we classified populations as rear-edge if the study area was in the lower 5th percentile of each species' range. For subspecies, we also consulted publicly available species range: maps (Fink et al. 2023). Range: maps for all species can be found in the data repository associated with this manuscript. We restricted analyses to species detected at least 50 times over the 10 years of sampling because data on rare species provide little information about population trends.

We modeled abundance of each species in year 1 (2014) as a function of growing degree-days, annual precipitation, and watershed soil moisture at each site in the previous year (2013).

The model for the first time period was:

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

$$\log\left(\psi_{i,k,1}\right) = \beta^{\psi}_{0,k} + \beta^{\psi}_{1,k}\text{Degree Days}_{i,1} + \beta^{\psi}_{2,k}\text{Precip}_{i,1} + \beta^{\psi}_{3,k}\text{Soil Moisture}_{\text{i}} \tag{2}$$

where $N_{i,k,1}$ is the abundance of species k at site i in year 1. The species-specific coefficients in Equation (1) were modeled as normally-distributed random effects on the log scale: $\beta_{q,k} \sim Normal\left(\bar{\beta}_{q,k}, \sigma^2_{q,\ k}\right)$. We used the species-specific coefficients in Equation (2) as a proxy for each species' relationship to temperature and precipitation and to categorize species as "warm-adapted" or "cool-adapted." The expected value $(\bar{\beta}_{q,k})$ for each species-specific coefficient $(q = 0, \ldots, 3)$ was described by fixed effects of range: position and migratory strategy.

$$\bar{\beta}_{q,k} = \alpha_{q,0} + \alpha_{q,1}\text{Range}_k + \alpha_{q,2}\text{Migration}_k \tag{3}$$

This formulation allowed for species with shared traits to have similar relationships to environmental variables, while still accounting for variation between species.

For years $t > 1$, abundance of each species at each site was determined by the annual growth rate, $\lambda_{k,t}$. We modeled the yearly growth rate as a function of the prior breeding season's growing degree-days and the previous year's annual precipitation.

$$N_{i,k,t} \sim \text{Poisson}\left(\psi_{i,k,t}\right) \tag{4}$$

$$\psi_{i,k,t} = \lambda_{i,k,t}\psi_{i,k,t-1}$$

$$\log(\lambda_{i,k,t}) = \beta^{\lambda}_{0,k} + \beta^{\lambda}_{1,k}\text{Degree Days}_{i,\ t} + \beta^{\lambda}_{2,k}\text{Precip}_{i,t}$$

Here again, the coefficients were modeled as random effects determined by guild structure, using the same formulation as in Equation (3). We modeled yearly abundance as a function of the previous year's expected abundance (ψ), rather than realized abundance (N), to allow for the possibility of local colonization (Hostetler and Chandler 2015). After analysis, we used the average percent change in abundance between years to classify each species as decreasing, stable or increasing in abundance. Rear-edge populations with declining abundance were further classified as trailing-edge populations.

Species richness at site i in year t was calculated as the realized number of species present at the site: $S_{i,t} = \sum_{k=1}^{K} I\left(N_{i,k,t} > 0\right)$. For each location, we also calculated the proportion of richness attributable to rear-edge species.

Observation Model

Birds are often not detected when present because they either do not vocalize during the survey period (i.e., are not available for detection) or their vocalizations are too far from the observer to be heard. We modeled both types of observation error using a hybrid distance sampling and removal sampling approach (Amundson et al. 2014). Let p^a_k denote availability (probability of an individual singing during the sampling period), and let $p^d_{i,k,t}$ be the probability of detecting an individual given it was present and available. We modeled the total number of individuals of each species observed at each site as the outcome of a binomial distribution: $n_{i,k,t} \sim \text{Binomial}\left(N_{i,k,t}, p^a_k p^d\right)$, with p^a_k modeled as a random effect following a logit-normal distribution: $\text{logit}\left(p^a_k\right) \sim \text{Normal}\left(1, \kappa\right)$. This prior was chosen to improve model convergence and avoid unrealistically low values of availability for less abundant species. We modeled the number of individuals first detected in each point-count survey time interval, $C_{1,k,t,1:4}$, as a categorical distribution:

$$C_{i,k,t,1:4} \sim \text{Categorical}\left(\frac{p^a_k}{\pi_k}, \frac{p^a_k\left(1-p^a_k\right)}{\pi_k}, \frac{p^a_k\left(1-p^a_k\right)^2}{\pi_k}, \frac{p^a_k\left(1-p^a_k\right)^3}{\pi_k}\right) \tag{5}$$

where π_k is the probability of being detected in at least one time interval.

To calculate distance-based detection probability, $p^d_{i,k,t}$, we truncated observations to a 100 m radius (Buckland et al. 2001) and grouped all detections into 10, 10-m distance bins (b in $b = 1, \ldots, B$). To estimate the effect of distance on detection, we used a half-normal detection function with scale parameter δ, which was assumed to vary with the noise level recorded at each site:

$$\log\left(\delta_{i,k,t}\right) = \beta_{4,k} + \beta_{5,k}\text{noise}_{i,t} \tag{6}$$

We fit models using Bayesian methods in NIMBLE (v. 0.10.1) via the *rnimble* package in R (de Valpine et al. 2017, NIMBLE Development Team 2019, R Core Team 2019). Prior to analysis, we standardized each continuous covariate by subtracting the mean and dividing by the standard deviation. We ran 100,000 Markov chain Monte Carlo (MCMC) iterations using 3 parallel chains with a burn-in of 90,000, resulting in 10,000 posterior samples. We assessed convergence of Markov chains using the Gelman-Rubin statistic (Gelman and Rubin 1992) and visual inspection. We evaluated goodness-of-fit for the observation process for each species using chi-squared tests (categorical data) and posterior P-values (binomial count data) (Gelman et al. 1996).

RESULTS

Across 10 years of sampling, we detected 33,125 birds representing 92 species, of which 25 species had at least 50 detections (Table 1). The majority (16) of species were at the core of their breeding range: (hereafter, "core populations"), whereas 9 species were at the rear-edge of their ranges (hereafter, "rear-edge populations"). Members of each core population were detected at an average of 88 sites (range: 47–108), with a mean of 43 (range: 10–157) detections per species per year. Rear-edge populations were detected at an average of 65 sites (range: 22–109), with a mean 43 (range: 7–91) detections per species per year.

Temperatures were highest in 2017 with an average May temperature of 16.1°C at the lowest elevations and 12.6°C at the highest elevations. Temperatures were lowest in 2018 with average temperatures ranging from 12.1 to 8.7°C across the elevational gradient. Low temperatures coincided with heavy rains, with a total precipitation of 12.6 cm at elevations above 1300 m and 8.7 cm at sites below 800 m in 2018. However, there was no correlation between temperature and precipitation over time ($r = -0.07$, $P = 0.84$). The driest year was 2016, with total precipitation ranging from 4.8 cm at the highest elevations to 3.3 mm at the lowest elevation. Annual precipitation steadily increased in the study area over the past 30 years (Supplementary Material Figure S1). There was no trend in May growing degree-days during the study period, though prior to 2020, average May temperature showed a positive trend.

Of the 25 species in our study, 21 species had stable or increasing populations (Figure 2). Declines were more common in rear-edge populations than those in the core of their range (Table 1). Three of nine rear-edge populations declined in abundance during the study period and were designated as trailing-edge populations. In contrast, only 1 of 16 of the core populations declined (Supplementary Material Figure S2). There were no rear-edge populations with increasing abundance or occupancy (Figure 2). For populations at the range: core, 11 species increased in abundance, with all but 3 species (*Pipilo erythrophthalmus* [Eastern Towhee]), *Contopus virens* [Eastern Wood-Pewee], and *Hylocichla mustelina* [Wood Thrush]) also increasing in site occupancy.

Species with a positive relationship to temperature and a negative relationship to precipitation were more likely to have stable or increasing populations (Figure 3). The largest declines in abundance were seen in long-distance migrants, with an average −0.85% yearly change in abundance (Figure 2). Short-distance migrants and resident species had an average

TABLE 1. Species with at least 50 detections from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA. Trend values >0 indicate the population is increasing, whereas values of <0 indicate the population is declining. Rear-edge populations with declining abundance trends are classified as trailing-edge.

Range	Scientific name	Common name	Species code	Migratory strategy	Abundance trend
Core	*Mniotilta varia*	Black-and-white Warbler	BAWW	Long-distance	0.03 (0.01 to 0.06)*
	Cyanocitta cristata	Blue Jay	BLJA	Resident	0.07 (0.03 to 0.12)*
	Poecile carolinensis	Carolina Chickadee	CACH	Resident	0.03 (−0.02 to 0.08)
	Pipilo erythrophthalmus	Eastern Towhee	EATO	Short-distance	−0.04 (−0.07 to 0.00)*
	Contopus virens	Eastern Wood-Pewee	EAWP	Long-distance	−0.04 (−0.11 to 0.04)
	Leuconotopicus villosus	Hairy Woodpecker	HAWO	Resident	0.11 (0.01 to 0.25)*
	Setophaga citrina	Hooded Warbler	HOWA	Long-distance	0.04 (0.01 to 0.07)*
	Setophaga americana	Northern Parula	NOPA	Short-distance	0.11 (0.06 to 0.20)*
	Seiurus aurocapilla	Ovenbird	OVEN	Long-distance	0.02 (0.00 to 0.04)*
	Dryocopus pileatus	Pileated Woodpecker	PIWO	Resident	0.09 (0.04 to 0.16)*
	Vireo olivaceus	Red-eyed Vireo	REVI	Long-distance	0.06 (0.03 to 0.10)*
	Piranga olivacea	Scarlet Tanager	SCTA	Long-distance	0.01 (−0.02 to 0.04)
	Baeolophus bicolor	Tufted Titmouse	TUTI	Resident	0.03 (0 to 0.07)*
	Sitta carolinensis	White-breasted Nuthatch	WBNU	Resident	0.11 (0.02 to 0.23)*
	Helmitheros vermivorum	Worm-eating Warbler	WEWA	Long-distance	0.10 (0.02 to 0.22)*
	Hylocichla mustelina	Wood Thrush	WOTH	Long-distance	−0.01 (−0.05 to 0.02)
Rear	*Vireo solitarius*	Blue-headed Vireo	BHVI	Short-distance	0 (−0.03 to 0.04)
	Setophaga fusca	Blackburnian Warbler	BLBW	Long-distance	−0.04 (−0.12 to 0.07)
	Setophaga virens	Black-throated Green Warbler	BTNW	Long-distance	−0.01 (−0.05 to 0.05)
	Pheucticus ludovicianus	Rose-breasted Grosbeak	RBGR	Long-distance	0.01 (−0.05 to 0.07)
	Junco hyemalis	Slate-colored Junco	SCJU	Short-distance	−0.03 (−0.06 to 0.01)
	Troglodytes hiemalis	Winter Wren	WIWR	Short-distance	0.03 (−0.07 to 0.24)
Trailing	*Setophaga caerulescens*	Black-throated Blue Warbler	BTBW	Long-distance	−0.06 (−0.08 to −0.03)*
	Cardellina canadensis	Canada Warbler	CAWA	Long-distance	−0.1 (−0.13 to −0.06)*
	Catharus fuscescens	Veery	VEER	Long-distance	−0.08 (−0.12 to −0.05)*

*Trends with 95% CIs excluding zero are indicated by an asterisk.

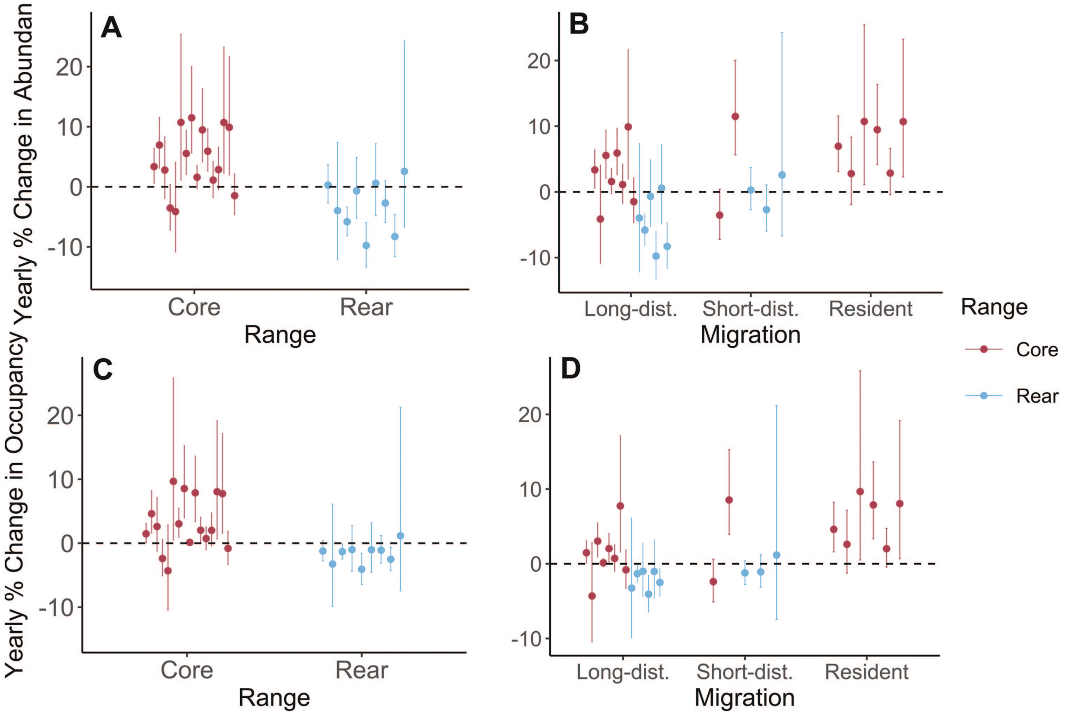

FIGURE 2. Average percent yearly change in (**A** and **B**) abundance and (**C** and **D**) occupancy from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA with species grouped by range position and migratory strategy. Rear-edge populations are shown in blue, with core populations shown in red. Estimates are posterior means (points) and 95% CIs.

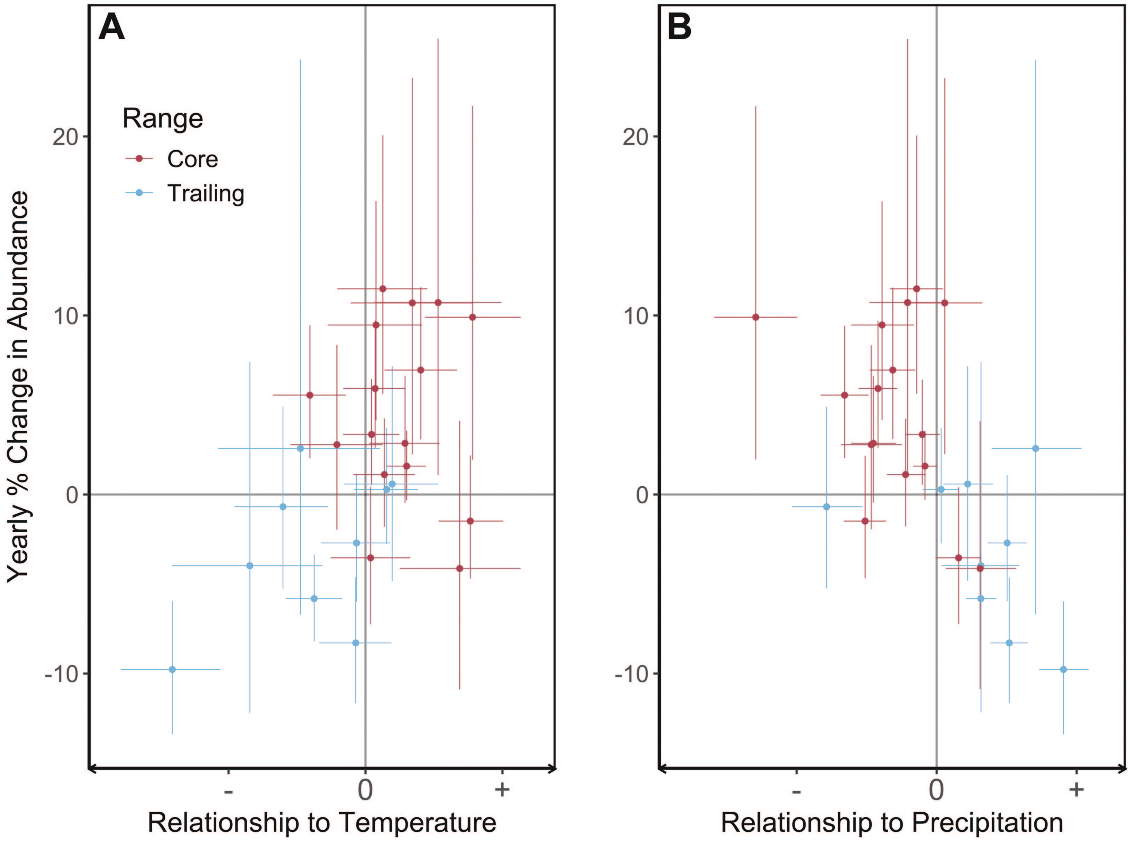

FIGURE 3. Average percent yearly change in abundance from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA with species grouped by relationship to (**A**) temperature and (**B**) precipitation. Rear-edge populations are shown in blue, with core populations shown in red. Relationship to temperature and precipitation are shown as the estimated effects of temperature and precipitation on species abundances in the first year of the study (2014).

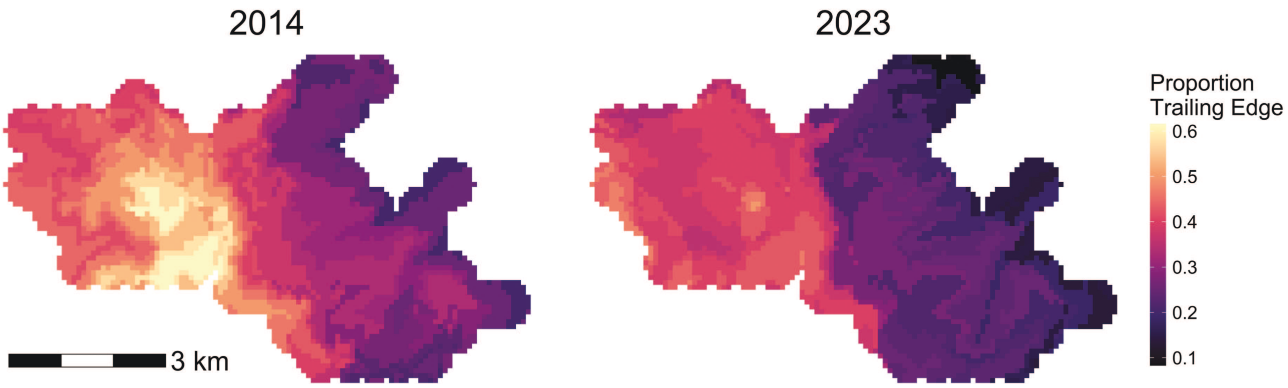

FIGURE 4. Proportion of species richness comprised of rear-edge populations in the Nantahala National Forest, North Carolina, USA in 2014 (left) and 2023 (right). Lighter colors indicate a higher proportion of species at the rear-edge of their range.

1.4% and 7.3% yearly increase in abundance, respectively, throughout the study period.

Species richness ranged from 11 to 19 species ha^{-1} and was lowest above 1,300 m (Supplementary Material Figure S3). At sites above 1,300 m, species composition was initially dominated by rear-edge populations (up to 61% rear-edge populations at some locations in 2014), transitioning to a majority of core populations in later years (average 40% rear-edge populations in 2023). At mid-elevation (1,000–1,300 m) sites, rear-edge populations contributed an average of 38% of species richness in 2014 compared to 27% by 2023 (Figure 4).

Goodness-of-fit tests demonstrated reasonable fit of the observation model. For the time-removal data, the median chi-squared *P*-value was 0.92 (range: 0.74–0.99), suggesting the distribution for the interval of first detection matched the expected distribution for all species. Similarly, we found a median chi-squared *P*-value of 0.94 (range: 0.79–0.99) for the distance sampling data. Posterior *P*-values for the count data (the total number of individuals of each species detected at each point-count) suggested a reasonable fit for most species, with a median value of 0.76 (range: 0.66–0.97). However, *P*-values indicated that the observation model for *Setophaga* *fusca* (Blackburnian Warbler), *C. virens*, *Leuconotopicus villosus* (Hairy Woodpecker), and *Troglodytes hiemalis* (Winter Wren) consistently overestimated the true number of individuals detected.

DISCUSSION

Most models of climate change impacts on species distributions predict shifts towards higher elevations and latitudes (Walther et al. 2002, Parmesan and Yohe 2003, McLachlan et al. 2005). Using one of the first community-level assessments of the consequences of trailing-edge population declines, we found support for the hypothesis that cool-adapted species near their low-latitude range: margins would exhibit population declines as warm-adapted species near the core of their range: expand their ranges into cooler climates at higher elevations. However, we found that declines of cool-adapted rear-edge populations were slower than the rate of encroachment by warm-adapted core populations. Thus, community turnover, at least among the most abundant species, may lag behind changes in community composition.

Continued declines of rear-edge populations could result in large changes to community composition and decreased species richness. Ecosystem-level impacts of changes in community composition are difficult to predict, but many ecological processes, such as nutrient cycling and predator prey dynamics, are a direct result of functional diversity within communities (Chapin III et al. 2000, Sekercioğlu et al. 2004). For example, in the boreal forests of North America, trailing-edge populations of seed-caching species such as *Perisoreus canadensis* (Canada Jay) and *Poecile hudsonicus* (Boreal Chickadee) can play a critical role in oak and pine tree dispersal (Koenig and Knops 2001, Sekercioğlu et al. 2004, Ralston et al. 2019). Loss of trailing-edge species may also decrease genetic diversity (Harrison 2020). Peripheral populations often harbor genotypes that are better adapted to climate extremes relative to populations in the core of the range: (Hampe and Petit 2005, Rehm et al. 2015). Therefore, the loss of locally adapted populations may not only alter local community composition, but further reduce range-wide adaptive capacity (Rehm et al. 2015).

Consistent with previous research, the negative impacts from increasing temperatures were most pronounced for species associated with cool climates (Rodenhouse et al. 2008, Pearce-Higgins et al. 2015). Species with a wide climate niche breadth may be less immediately affected by warming temperatures, in part because climate generalists (i.e., species without a strong association to temperature) are often habitat generalists (Davey et al. 2013, Godet et al. 2015, Sweeney and Jarzyna 2022). Though low-latitude, peripheral populations can demonstrate high degrees of local adaptation and resilience to less favorable conditions (e.g., high temperatures) (Hampe and Petit 2005, Bennett et al. 2015), these adaptations are unlikely to prevent population declines. In addition to increasing temperature, latitudinal range: shifts of warm-adapted species may introduce novel competitive interactions (McDonald et al. 2012, Gibson-Reinemer and Rahel 2015), which invading warm-adapted species are more likely to win (Urban et al. 2012). As temperatures continue to rise, communities with a high proportion of cool-adapted, rear-edge species will likely transition to communities dominated by warm-adapted species.

Although several rear-edge populations declined during the 10 years of investigation, none of the species in our study declined to local extinction. Thus, as warm-adapted, core populations shifted upward in elevation, species richness increased, particularly at high elevations. Differential population growth rates of cool and warm-adapted species can create short-term trends of increasing species richness (Urban et al. 2012), masking signs of long-term biodiversity loss and extinction debt (Tilman et al. 1994, Ewers and Didham 2006, Urban et al. 2012). However, elevated levels of species richness are usually temporary (Tilman et al. 1994, Hampe and Petit 2005, Habibzadeh et al. 2021), suggesting subsequent reductions in species abundance and richness in the near future (Ewers and Didham 2006, Halley and Pimm 2023).

In the early years of the study, the majority of species present at high-elevation sites were at the edge of their range, but this proportion decreased in later years. Combined with the increases in species richness observed at almost all sites, these results suggest a trend towards homogenization of the bird community across the elevation gradient. Homogenization can increase vulnerability to environmental disturbance (Olden and Poff 2004, Catano et al. 2020), especially if members of the homogenized community compete for resources (Davey et al. 2012). While the ecosystem ramifications of increased prevalence of species in the core of their range: remains an open question, homogenization of the bird community is likely to occur if rear-edge populations continue to decline.

Climate change may threaten cool-adapted species by reducing available habitat and fragmenting populations into isolated habitat patches (Abeli et al. 2018, Habibzadeh et al. 2021). Many trailing-edge populations are confined to fragmented high-elevation habitat (Habibzadeh et al. 2021), and thus latitudinal range: shifts would require long-distance dispersal to other suitable "sky islands." Long-distance dispersal is notoriously difficult to study, but there is scant evidence that long-distance neotropical migratory passerines disperse more than a few kilometers between breeding sites (Faaborg et al. 2010, Årevall et al. 2018, Vilà-Cabrera et al. 2019). Though not investigated here, dispersal limitations may prevent climate tracking even after habitat quality declines below optimal conditions (Hampe and Petit 2005, Bennett et al. 2015, Gaya et al. 2024), concentrating populations into small habitat patches and temporarily increasing population densities and species richness (Collinge 1998).

In contrast to the congruence of our results with predictions of climate change impacts, several studies have found unexpected latitudinal and elevational changes in species distributions (Tingley et al. 2012, Freeman et al. 2018a, Rubenstein et al. 2023). There are several possible explanations for the agreement of our findings with predictions from climate change models. Numerous studies suggest the strength of climate-induced range: shifts are strongly species and region specific (La Sorte and Jetz 2012, Thompson and Fronhofer 2019). For instance, several passerine species in California have demonstrated downhill movements as increasing precipitation pulled species downslope while rising temperatures pushed species in the opposite direction (Tingley et al. 2012). Fragmented habitat can also play a role in climate-induced shifts, Species with limited dispersal options may show delayed responses to environmental changes (Ewers and Didham 2006, Platts et al. 2019). Finally, the southern Appalachian Mountains harbor a high proportion of Neotropical migrants, which tend to have shorter life spans than resident species (Soriano-Redondo et al. 2020), and rapid range: shifts are more likely to be observed in species with shorter life expectancy (Tingley et al. 2012, Couet et al. 2022).

Modeling the direction and velocity of range: shifts remains a difficult task and most trait-based range: forecasts have poor predictive power (Angert et al. 2011, Auer and King 2014, Hovick et al. 2016). Research on migratory strategies has been mixed, with some studies demonstrating no difference between migratory strategies (Sekercioğlu 2007, Angert et al. 2011, Hovick et al. 2016), whereas others have noted significantly reduced range: expansion in long-distance migrants (Laaksonen and Lehikoinen 2013, Rushing et al. 2020). We found migratory status was a mediocre predictor of range: shifts; however, when used in concert with range: position, long-distance migrants had lower average percent change in abundance than resident species. We also found that all but one of the studied long-distance rear-edge populations had a negative relationship with temperature, while the reverse was true for range-core populations. These results suggest that individual populations' range: position (edge vs core) and life history traits are likely better predictors of a species' capacity for climate-induced range: shifts.

Although air temperatures have generally increased in our study area since 2002 (Lewis et al. 2022), several years of cold temperatures after 2020 obscured the trend. Increased climate variation may pose a greater threat to species persistence than increased mean temperature (Vasseur et al. 2014), but there is often a delay between temperature change and changes in species composition (Godet et al. 2011, Devictor et al. 2012, Lindström et al. 2013). Many species are resilient to occasional fluctuations in climate, only moving uphill or adjusting behaviors after repeated exposure to extreme conditions (Cohen et al. 2020). While several species appeared to be responding to changing temperatures, longer-term data sets (>10 years) may be necessary to fully reveal the connection between breeding season weather variables and interannual changes in abundance.

The high proportion of stable or increasing species in our study may in part be the result of our inability to model the dynamics of rare species. We only modeled species with greater than 50 aural detections to ensure the model had a reasonable sample size for estimating yearly changes (Buckland et al. 2001). By focusing only on species detected by sound, we removed a source of variability in our detection model, but also removed most female individuals (who are less likely to vocalize) as well as all raptors and owls, which were more frequently seen than heard in our study area. Moreover, we likely excluded lower abundance species that may have shown declines during our study. For instance, *Empidonax virescens* (Acadian Flycatcher) and *Setophaga pensylvanica* (Chestnut-sided Warbler) are both present at the study site and are declining in the southern Appalachian Mountains (Sauer et al. 2017), but were excluded from the study due to low detection. Thus, while our study reveals a clear trend of stability for the most common species at the core of their range, rare or elusive species in this community may deviate from this pattern.

Although rear-edge populations continued to persist, if rates of population declines continue, local extinctions will follow. The implications of local extinction depend on the underlying demographic processes. If declines of trailing-edge populations are the result of directional dispersal towards cooler climates at higher latitudes, trailing-edge genetic diversity may be conserved (Hargreaves and Eckert 2014). In contrast, if uphill movements represent an "escalator to extinction" as survival and reproductive rates decline (Sekercioğlu et al. 2008, Freeman et al. 2018b), then trailing-edge range: retractions may greatly reduce species-level genetic diversity. Future studies should focus on the demographic drivers of peripheral population dynamics (Chandler et al. 2018), as well as the ecosystem-level consequences of losing these unique populations in regions formerly characterized as trailing-edge hotspots.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

We did not physically touch any species for this study. However, the larger study under which this research was conducted was approved by the University of Georgia's Animal Care and Use Committee (Permit A2022 11-007-Y1-A0).

Author contributions

H.G and R.C. jointly conceived the model. Coding and data analysis were performed by H.G, with supervision from R.C. Both H.G. and R.C. contributed to manuscript writing and interpretation of results.

Data availability

All code to reproduce all analysis is publicly available at Gaya and Chandler (2024).

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