

# Warm-adapted encroachment outpaces cool-adapted retreat in a hotspot of trailing-edge population diversity

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## 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 on Zenodo:  
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### Abstract

Many populations near low-latitude range margins are declining in response to climate change, but most studies of trailing-edge populations have focused on single species. Using ten years (2014–2023) of avian survey data from a trailing-edge population hotspot in the Appalachian Mountains, USA, we tested the hypothesis that high-elevation communities would experience turnover through thermophilisation, 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 populations decreased in abundance whereas six species exhibited little change. For warm-adapted populations, one of 16 decreased in abundance, 11 increased, and four exhibited no change. Our results indicate that warm-adapted species are expanding their ranges faster than the rate at which ranges of cool-adapted species are contracting, suggesting that community turnover will lag behind encroachment by warm-adapted species.

## 1 Introduction

Population-level extinction risk from climate change is predicted to be highest at low-latitude range margins (Hampe & Petit, 2005; Sekercioğlu *et al.*, 2008; Rushing *et al.*, 2020; Stevens *et al.*, 2023b) where species frequently occur near their 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 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 & Chandler, 2020). However, most research on trailing-edge populations 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

13 impacted by climate change in numerous ways. If cool-adapted species at the edge of their  
14 range decline precipitously as warm-adapted populations encroach, complete community  
15 turnover could be possible through a process known as thermophilisation (Hampe & Petit,  
16 2005; Sunday *et al.*, 2012; Khaliq *et al.*, 2024). Alternatively, if invasion by warm-adapted  
17 species happens faster than the retreat of cool-adapted species, rising temperatures could  
18 lead to increased species richness, even as trailing-edge populations decline (Lemoine &  
19 Böhning-Gaese, 2003; La Sorte *et al.*, 2009; Davey *et al.*, 2012). Under this scenario, species  
20 richness might increase, but species composition will be greatly altered.

21 The speed of community encroachment by warm-adapted species, and the rate of decline  
22 of cool-adapted species, may depend on species-level traits other than thermal tolerance. For  
23 instance, the ranges of short-lived species often shift upwards in elevation faster under cli-  
24 mate change than long-lived species (Couet *et al.*, 2022). In avian communities, long-distance  
25 neotropical migrants shift their cold-edge range boundaries slower than short-distance mi-  
26 grants or resident species (Rushing *et al.*, 2020; Välimäki *et al.*, 2016; Stevens *et al.*, 2023a).  
27 Many migratory species have a slower phenological response to ongoing climate warming  
28 than resident species, which may translate to a reduced competitive advantage on the breed-  
29 ing ground (Wittwer *et al.*, 2015; MacLean & Beissinger, 2017). Thus, extinction risk may  
30 be higher for trailing-edge populations of migratory species than resident species.

31 We used 10 years of avian survey data from a hotspot of trailing-edge population diver-  
32 sity (Merker & Chandler, 2020) in the southern Appalachian Mountains to (1) assess the  
33 generality of trailing-edge population declines, and (2) determine the consequences for com-  
34 munity structure. We predicted species-specific shifts in abundance and occupancy would  
35 depend on range-position, migratory strategy and climate niche breadth. We predicted that  
36 cool-adapted trailing-edge populations would decrease in abundance and become increas-  
37 ingly restricted to high elevations. In contrast, we predicted that warm-adapted species near  
38 the center of their geographic ranges would increase in abundance and expand their distri-  
39 butions upwards in elevation. We further predicted long-distance migratory species would

40 have slower rates of local range shifts than short-distance migrants or residents.

## 41 **2 Methods**

### 42 **Study Area**

43 The Nantahala National Forest in the southern Appalachian Mountains contains a high  
44 diversity of species at the trailing-edge of their breeding range (Merker & Chandler, 2020).  
45 Elevation within the region ranges from 660–1590 m (Figure 1), with drier conditions found  
46 on the steeper, more exposed slopes in the eastern portion of the study area. High elevation  
47 sites are cooler than those at lower elevations, with an average May temperature of 10.5°C  
48 above 1300 m, compared to 14°C at 700 m. During the breeding season (May – July), sites  
49 above 1300 m receive an average 26.4 cm of precipitation in comparison to only 18.2 cm of  
50 precipitation at the lowest elevations in the study area (Miniat *et al.*, 2022).

51 Dominant and subdominant tree species include oaks (*Quercus spp.*), hickory (*Carya*  
52 *spp.*), yellow poplar (*Liriodendron tulipifera*), birch (*Betula spp.*) maple (*Acer spp.*), fraser  
53 magnolia (*Magnolia fraseri*), and common buckeye (*Aesculus flava*). Serviceberry (*Ame-*  
54 *lanchier spp.*) and witchhazel (*Hamamelis virginiana*) are common in the mid-story. Follow-  
55 ing declines of American chestnut (*Castanea dentata*) and Eastern hemlock (*Tsuga canad-*  
56 *ensis*), rhododendron (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), and huck-  
57 leberry (*Vaccinium spp.* and *Gaylussacia spp.*) have become more common in the understory  
58 and in forest gaps (Elliott & Swank, 2008).

### 59 **Environmental Data**

60 We calculated total annual precipitation for each year (2013–2022) based on nine USDA  
61 Forest Service (USFS) climate stations (Miniat *et al.*, 2022), and we used interpolations of  
62 PRISM data (Daly *et al.*, 2008) to create smoothed precipitation layers spanning the study  
63 area. To represent the heat accumulation during the breeding season, we calculated growing

64 degree-days (Lany *et al.*, 2016; Cesaraccio *et al.*, 2001) in May of each year (2013–2022).  
65 For many species in the southern Appalachian Mountains, May represents a critical part of  
66 the breeding season when birds build nests and begin provisioning fledglings (Lumpkin &  
67 Pearson, 2013; Lewis *et al.*, 2023). Temperature data were collected hourly from 34 temper-  
68 ature loggers (Onset Computer Corp., Bourne, MA, model number UA-002-64) distributed  
69 throughout the study area, as well as at 5 US Forest Service (USFS) climate stations (Miniat  
70 *et al.*, 2022). Mean temperature in May 2014–2022 ranged from 0.43–33.6°C, with a mean  
71 annual precipitation of 230.6 cm.

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

## 76 Surveys

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

## 84 Process Model

85 We analyzed point count data using dynamic multi-species N-mixture models (Alldredge  
86 *et al.*, 2007; Dail & Madsen, 2011; Amundson *et al.*, 2014). These models allow for the  
87 assessment of environmental effects on spatial and temporal variation in population growth  
88 rates while accounting for demographic stochasticity, serial correlation, and observation er-

ror arising from variation in detection probability. We categorized each species by migra-  
 tory strategy (resident, short-distant migrant, or long-distance migrant) and range position  
 (trailing-edge or core) to assess the effects of species traits on population trends. Range  
 position was determined using the classification in Merker & Chandler (2020) and 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 degree days,  
 annual precipitation, and soil moisture at each site in the previous year (2013).

The model for the first time period was:

$$N_{i,k,1} \sim \text{Poisson}(\psi_{i,k,1}) \quad (1)$$

$$\log(\psi_{i,k,1}) = \beta_{0,k}^\psi + \beta_{1,k}^\psi \text{DegreeDays}_{i,1} + \beta_{2,k}^\psi \text{Precip}_{i,1} + \beta_{3,k}^\psi \text{SoilMoisture}_i \quad (2)$$

where  $N_{i,k,1}$  is the abundance of species  $k$  at site  $i$  in year 1. The species-specific coefficients  
 in Eq. 2 were modeled as normally-distributed random effects on the log scale:  $\beta_{q,k} \sim$   
 $\text{Norm}(\bar{\beta}_{q,k}, \sigma_{q,k}^2)$ . To complement the analysis using the binary classification of species as  
 “warm-adapted” or “cool-adapted”, we used the species-specific coefficients in Eq. 2 as a  
 proxy for each species’ relationship to temperature and precipitation. The expected value  
 ( $\bar{\beta}_{q,k}$ ) for each species-specific coefficient ( $q = 0, \dots, 3$ ) was described by an intercept and  
 fixed effects of range position and migratory strategy.

$$\bar{\beta}_{q,k}^\psi = \alpha_{q,0} + \alpha_{q,1} \text{Range}_k + \alpha_{q,2} \text{Migration}_k \quad (3)$$

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 degree days and the previous year’s annual precipitation.

$$N_{i,k,t} \sim \text{Poisson}(\psi_{i,k,t})$$

$$\psi_{i,k,t} = \lambda_{i,k,t} \psi_{i,k,t-1} \quad (4)$$

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

109 Here again, the coefficients were modeled as random effects determined by guild structure,  
 110 using the same formulation as in Eq. 3. We modeled yearly abundance as a function of the  
 111 previous year's expected abundance ( $\psi$ ), rather than realized abundance ( $N$ ), to allow for  
 112 the possibility of local colonization (Hostetler & Chandler, 2015). After analysis, we used the  
 113 average percent change in abundance between years to classify each species as decreasing,  
 114 stable or increasing in abundance.

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

## 118 Observation Model

119 Birds are often not detected when present because they either do not vocalize during the  
 120 survey period (i.e., are not available for detection) or their vocalizations are too far from the  
 121 observer to be heard. We modeled both types of observation error using a hybrid distance  
 122 sampling and removal sampling approach Amundson *et al.* (2014). Let  $p_k^a$  denote availability  
 123 (probability of an individual singing during the sampling period), and let  $p_{i,k,t}^d$  be the prob-  
 124 ability of detecting an individual given it was present and available. We modeled the total  
 125 number of individuals of each species observed at each site as the outcome of a binomial  
 126 distribution:  $n_{i,k,t} \sim \text{Binomial}(N_{i,k,t}, p_k^a p_{i,k,t}^d)$ , with  $p_k^a$  modeled as a random effect following a  
 127 logit-normal distribution:  $\text{logit}(p_k^a) \sim \text{Normal}(1, \kappa)$ .

128 To calculate distance-based detection probability, we truncated observations to a 100  
 129 m radius (Buckland *et al.*, 2001) and grouped all detections into 10, 10-m distance bins ( $b$   
 130 in  $b = 1, \dots, B$ ). To estimate the effect of distance on detection, we used a half-normal

131 detection function with scale parameter  $\delta$ .

$$\log(\delta_{i,k,t}) = \beta_{0,k}^d + \beta_{1,k}^d \text{noise}_{i,t}$$

132 We fit models using Bayesian methods in NIMBLE (v. 0.10.1) via the ‘rnimble’ package in  
133 R (de Valpine *et al.*, 2017; NIMBLE Development Team, 2019; R Core Team, 2019). Prior to  
134 analysis, we standardized each continuous covariate by subtracting the mean and dividing by  
135 the standard deviation. We ran 100,000 MCMC iterations using three parallel chains with a  
136 burn-in of 90,000, resulting in 10,000 posterior samples. We assessed convergence of Markov  
137 chains using the Gelman-Rubin statistic (Gelman & Rubin, 1992) and visual inspection.

### 138 **3 Results**

139 Across 10 years of sampling, we detected 33,125 birds representing 92 species, of which 25  
140 species had at least 50 detections (Table 1). The majority (16) of species were at the core of  
141 their breeding range (hereafter, “core populations”), whereas 9 species were at the trailing-  
142 edge of their ranges (hereafter, “trailing-edge populations”). Each core species was detected  
143 at an average of 88 sites (range 47 – 108), with a mean 43 (range 10 – 157) detections per  
144 species per year. Trailing-edge species were detected at an average of 65 sites (range 22 –  
145 109), with a mean 43 (range 7 – 91) detections per species per year.

146 Temperatures were highest in 2017 with an average May temperature of 16.1°C at the  
147 lowest elevations and 12.6°C at the highest elevations. Temperatures were lowest in 2018  
148 with average temperatures ranging from 12.1–8.7 °C across the elevational gradient. Low  
149 temperatures coincided with heavy rains, with a total precipitation of 12.6 cm at elevations  
150 above 1300 m and 8.7 cm at sites below 800 m in 2018. However, there was no correlation  
151 between temperature and precipitation over time ( $r = -0.07$ ,  $p = 0.84$ ). The driest year was  
152 2016, with total precipitation ranging from 4.8 cm at the highest elevations to 3.3 mm at the  
153 lowest elevation. Annual precipitation steadily increased in the study area over the past 30

154 years (Figure S1). There was no trend in May degree days during the study period, though  
155 prior to 2020, average May temperature showed a positive trend (Lewis *et al.*, 2023).

156 Of the 25 species in our study, 21 species had stable or increasing populations (Figure  
157 2). Declines were more common in trailing-edge populations than those in the core of  
158 their range (Table 1). Three trailing-edge populations declined in abundance during the  
159 study period, compared with 1 core-species. There were no trailing-edge populations with  
160 increasing abundance or occupancy (Figure 3). For species at the range core, 11 species  
161 increased in abundance, with all but 3 species (eastern towhee, eastern wood-pewee and  
162 wood thrush) also increasing in site occupancy.

163 Species with a positive relationship to temperature and a negative relationship to pre-  
164 cipitation were more likely to have stable or increasing populations (Figure 4). The largest  
165 declines in abundance were seen in long-distance migrants, with an average -0.85 % yearly  
166 change in abundance. Short-distance migrants and resident species had an average 1.4% and  
167 7.3% yearly increase in abundance throughout the study period.

168 Species richness ranged from 11–19 species/ha and was lowest above 1300 m (Figure  
169 S2). At sites above 1300 m, species composition was initially dominated by trailing-edge  
170 populations (up to 61% trailing-edge populations at some locations in 2014), transitioning  
171 to a majority of core populations in later years (average 40% trailing-edge populations in  
172 2023). At mid elevation (1000 – 1300 m) sites, trailing-edge populations contributed an  
173 average of 38% of species richness in 2014 compared to 27% by 2023 (Figure 5).

## 174 4 Discussion

175 Most models of climate change impacts on species distributions predict shifts towards higher  
176 elevations and latitudes (Walther *et al.*, 2002; Parmesan & Yohe, 2003; McLachlan *et al.*,  
177 2005). Using one of the first community-level assessments of the consequences of trailing-  
178 edge population declines, we found support for the hypothesis that cool-adapted species near

179 their low-latitude range margins would exhibit population declines as warm-adapted species  
180 near the core of their range expand their ranges into cooler climates at higher elevations.  
181 However, we found that declines of trailing-edge populations were slower than the rate of  
182 encroachment by warm-adapted populations, and thus community turnover may lag behind  
183 changes in community composition.

184 Continued declines of trailing-edge populations will likely result in complete reorganiza-  
185 tion of community composition and decreased species richness. Ecosystem-level impacts of  
186 changes in community composition are difficult to predict, but many ecological processes,  
187 such as nutrient cycling and predator prey dynamics, are a direct result of functional diver-  
188 sity within communities (Chapin III *et al.*, 2000; Sekercioglu *et al.*, 2004). For example, in  
189 the boreal forests of North America, trailing-edge populations of seed-caching species such  
190 as Canada jays (*Perisoreus canadensis*) and boreal chickadees (*Poecile hudsonicus*) can play  
191 a critical role in oak and pine tree dispersal (Koenig & Knops, 2001; Sekercioglu *et al.*,  
192 2004; Ralston *et al.*, 2019). Loss of trailing-edge species may also decrease genetic diversity  
193 (Harrison, 2020). Trailing-edge populations often harbor genotypes that are better adapted  
194 to climate extremes relative to populations in the core of the range (Hampe & Petit, 2005;  
195 Rehm *et al.*, 2015). Therefore the loss of locally adapted populations may not only alter  
196 local community composition, but further threaten the range-wide adaptive capacity (Rehm  
197 *et al.*, 2015).

198 Consistent with previous research, the negative impacts from increasing temperatures  
199 were most pronounced for species associated with cool climates (Rodenhuse *et al.*, 2008;  
200 Pearce-Higgins *et al.*, 2015). Species with a wide climate niche breadth may be less imme-  
201 diately affected by warming temperatures, in part because climate generalists (i.e. species  
202 without a strong association to temperature) are often habitat generalists (Davey *et al.*, 2013;  
203 Godet *et al.*, 2015; Sweeney & Jarzyna, 2022). Though low-latitude, peripheral populations  
204 can demonstrate high degrees of local adaptation and resilience to less favorable conditions  
205 (e.g., high temperatures) (Hampe & Petit, 2005; Bennett *et al.*, 2015), these adaptations are

206 unlikely to prevent population declines. In addition to increasing temperature, latitudinal  
207 range shifts of warm-adapted species may introduce novel competitive interactions (McDon-  
208 ald *et al.*, 2012; Gibson-Reinemer & Rahel, 2015), which invading warm-adapted species are  
209 more likely to win (Urban *et al.*, 2012). As temperatures continue to rise, communities with  
210 a high proportion of trailing-edge species will likely transition to communities dominated by  
211 warm-adapted species.

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

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

230 Climate change may also threaten cool-adapted species by reducing available habitat and  
231 fragmenting populations into isolated habitat patches (Abeli *et al.*, 2018; Habibzadeh *et al.*,  
232 2021). Many trailing-edge populations are already confined to fragmented high-elevation

233 habitat (Habibzadeh *et al.*, 2021), and thus latitudinal range shifts would require long dis-  
234 tance dispersal to other suitable ‘sky islands’. Long-distance dispersal is notoriously difficult  
235 to study, but there is scant evidence that long-distance neotropical migratory passerines  
236 disperse more than a few kilometers between breeding sites (Faaborg *et al.*, 2010; Årevall  
237 *et al.*, 2018; Vilà-Cabrera *et al.*, 2019). Though not investigated here, dispersal limitations  
238 may prevent climate tracking even after habitat quality declines below optimal conditions  
239 (Hampe & Petit, 2005; Bennett *et al.*, 2015; Robinson *et al.*, 2015), concentrating popula-  
240 tions into small habitat patches and temporarily increasing population densities and species  
241 richness (Collinge, 1998).

242 In contrast to the congruence of our results with predictions of climate change impacts,  
243 several studies have found unexpected latitudinal and elevational changes in species distri-  
244 butions (Tingley *et al.*, 2012; Rubenstein *et al.*, 2023; Freeman *et al.*, 2018a). There are  
245 several possible explanations for the agreement of our findings with predictions from climate  
246 change models. Numerous studies suggest the strength of climate-induced range shifts is  
247 strongly species and region specific (La Sorte & Jetz, 2012; Thompson & Fronhofer, 2019).  
248 For instance, several passerine species in California have demonstrated downhill movements  
249 as increasing precipitation pulled species downslope while rising temperatures pushed species  
250 in the opposite direction (Tingley *et al.*, 2012). Fragmented habitat can also play a role in  
251 climate-induced shifts; Species with limited dispersal options may show delayed responses to  
252 environmental changes (Ewers & Didham, 2006; Platts *et al.*, 2019). Finally, the southern  
253 Appalachian Mountains harbor a high proportion of neotropical migrants, which tend to  
254 have shorter life spans than resident species (Soriano-Redondo *et al.*, 2020), and rapid range  
255 shifts are more likely to be observed in species with shorter life expectancy (Tingley *et al.*,  
256 2012; Couet *et al.*, 2022).

257 Modeling the direction and velocity of range shifts remains a difficult task and most trait-  
258 based range forecasts have poor predictive power (Angert *et al.*, 2011; Auer & King, 2014;  
259 Hovick *et al.*, 2016). Research on migratory strategies has been mixed, with some studies

260 demonstrating no difference between migratory strategies (Sekercioglu, 2007; Angert *et al.*,  
261 2011; Hovick *et al.*, 2016), while others have noted significantly reduced range expansion  
262 in long-distance migrants (Laaksonen & Lehikoinen, 2013; Rushing *et al.*, 2020). We found  
263 migratory status was a poor predictor of range shifts; however, when used in concert with  
264 range position, long-distance migrants had lower average percent change in abundance than  
265 resident species. We also found that all but one of the studied long-distance trailing-edge  
266 species had a negative relationship with temperature, while the reverse was true for range-  
267 core species. These results suggest that individual populations' range position (trailing vs  
268 core) and life history traits are likely better predictors of a species' capacity for climate-  
269 induced range shifts.

270 Although air temperatures have generally increased in our study area since 2002 (Lewis  
271 *et al.*, 2023), several years of cold temperatures after 2020 obscured the trend. Increased  
272 climate variation may pose a greater threat to species persistence than increased mean  
273 temperature (Vasseur *et al.*, 2014), but there is often a delay between temperature change  
274 and changes in species composition (Godet *et al.*, 2011; Devictor *et al.*, 2012; Lindström  
275 *et al.*, 2013). Many species are resilient to occasional fluctuations in climate, only moving  
276 uphill or adjusting behaviors after repeated exposure to extreme conditions (Cohen *et al.*,  
277 2020). While several species appeared to be responding to changing temperatures, longer-  
278 term data sets (>10 years) may be necessary to fully reveal the connection between breeding  
279 season weather variables and inter-annual changes in abundance.

280 Although trailing-edge populations continued to persist after encroachment by warm-  
281 adapted species, if rates of population declines continue, local extinctions will follow. The  
282 implications of local extinction depend on the underlying demographic processes. If declines  
283 of trailing-edge populations are the result of directional dispersal towards cooler climates  
284 at higher latitudes, trailing-edge genetic diversity may be conserved (Hargreaves & Eckert,  
285 2014). In contrast, if uphill movements represent an 'escalator to extinction' as survival and  
286 reproductive rates decline (Sekercioglu *et al.*, 2008; Freeman *et al.*, 2018b), then trailing-edge

287 range retractions may greatly reduce species-level genetic diversity. Future studies should  
288 focus on the demographic drivers of peripheral population dynamics (Chandler *et al.*, 2018),  
289 as well as the ecosystem-level consequences of losing these unique populations in regions  
290 formerly characterized as trailing-edge hotspots.

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

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

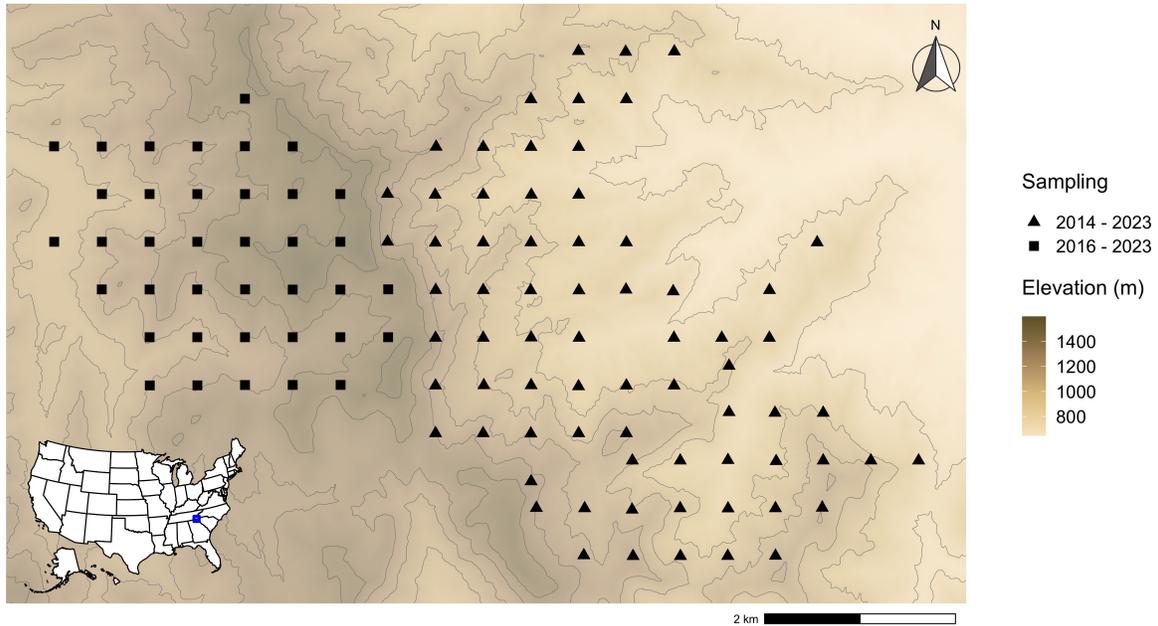


Figure 1: Map of point count locations in the Nantahala National Forest, North Carolina, USA. Points shown as triangles (right side) were surveyed from 2014-2023. Locations shown as squares (left side) were surveyed starting in 2016.

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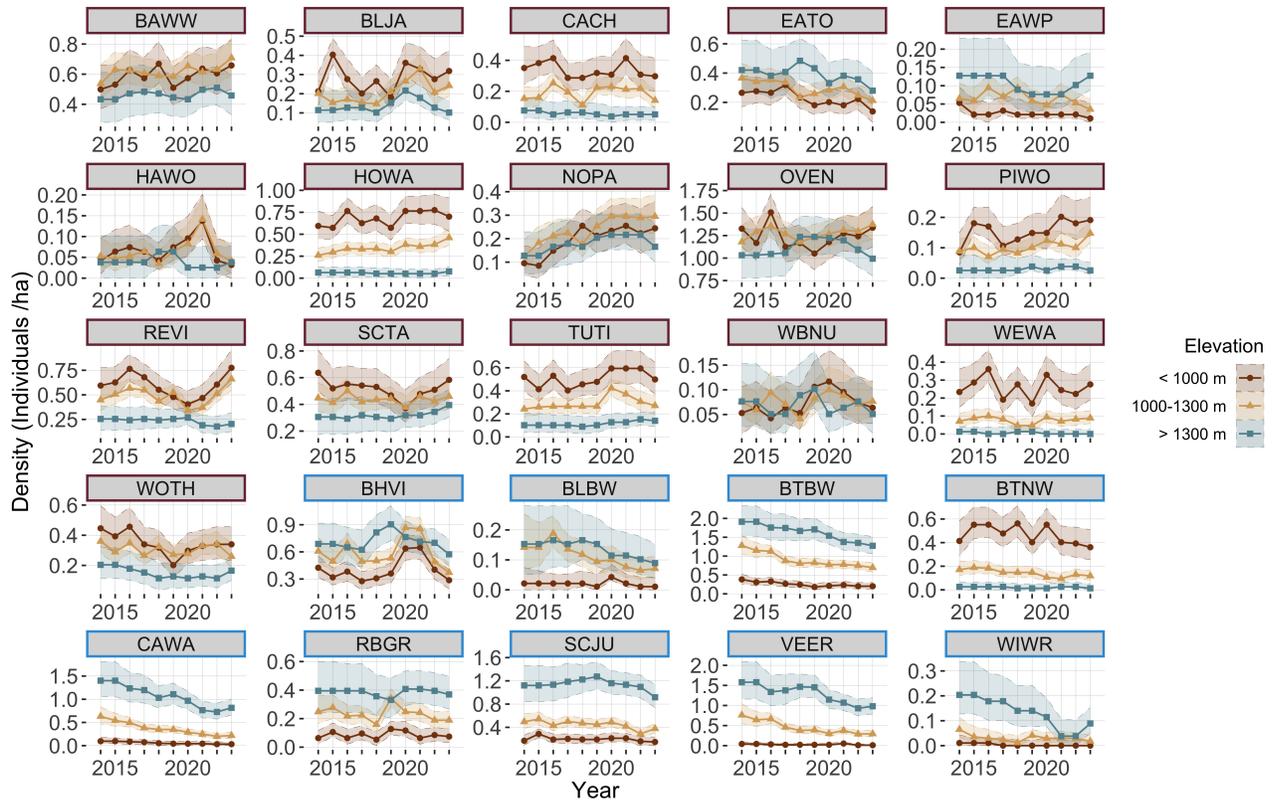


Figure 2: Temporal trends in population density at high, medium and low elevations. Estimates are the realized values of density averaged across sites within each elevation category. Point estimates are posterior means with 95% CIs. Species are sorted by range position. Headings for populations at the trailing-edge of the species' range are outlined in blue and headings for populations in the core of their range are outlined in red. The scale of the y-axis varies between species for clarity.

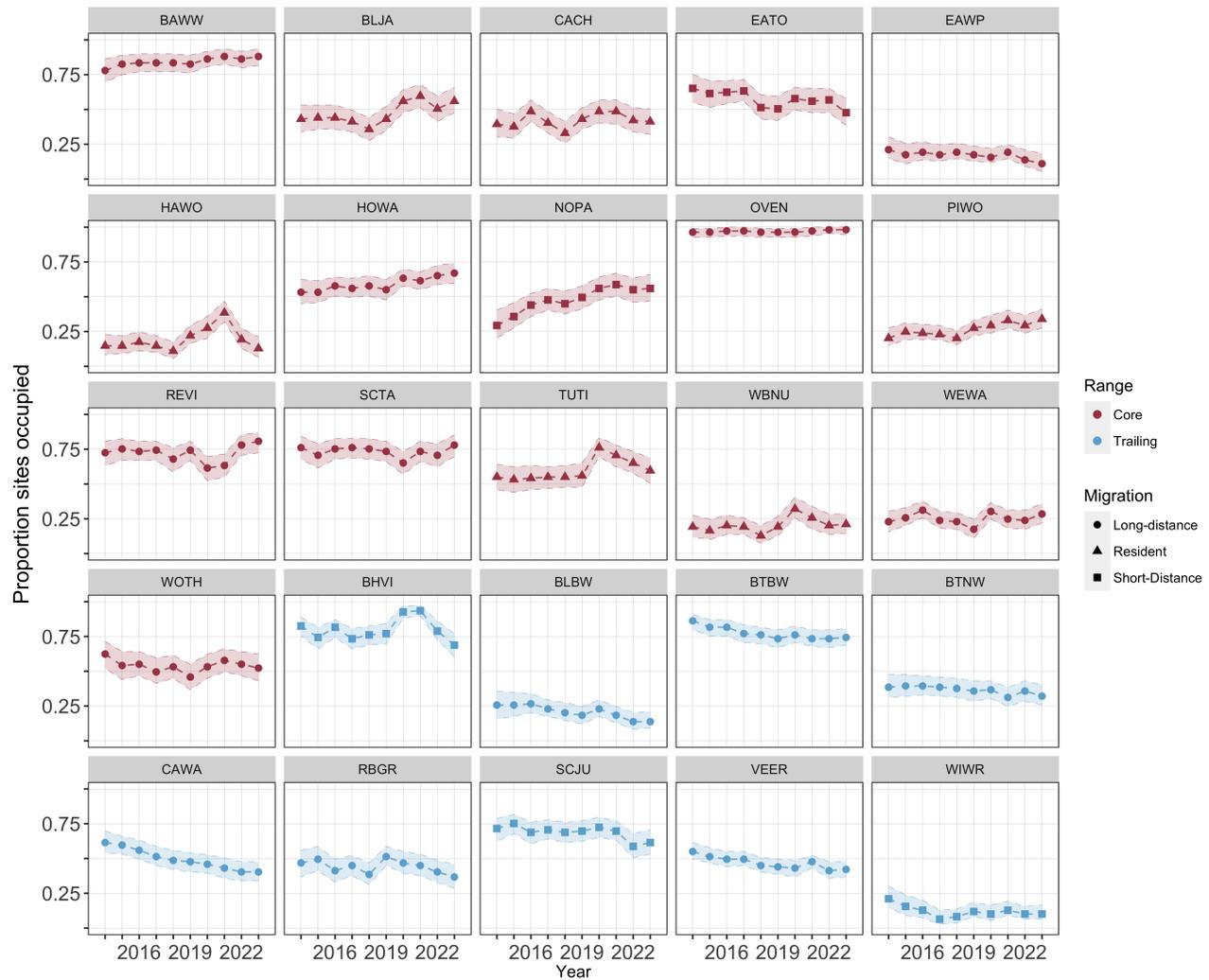


Figure 3: Site occupancy for species in the Nantahala National Forest, North Carolina, USA from 2014 to 2023. Estimates are posterior means (points) and 95% CIs. Species are sorted by range position with trailing-edge species in blue and core species in red. Point shapes indicate if a species is a long-distance migrant (circles), short-distance migrant (squares) or resident species (triangles).

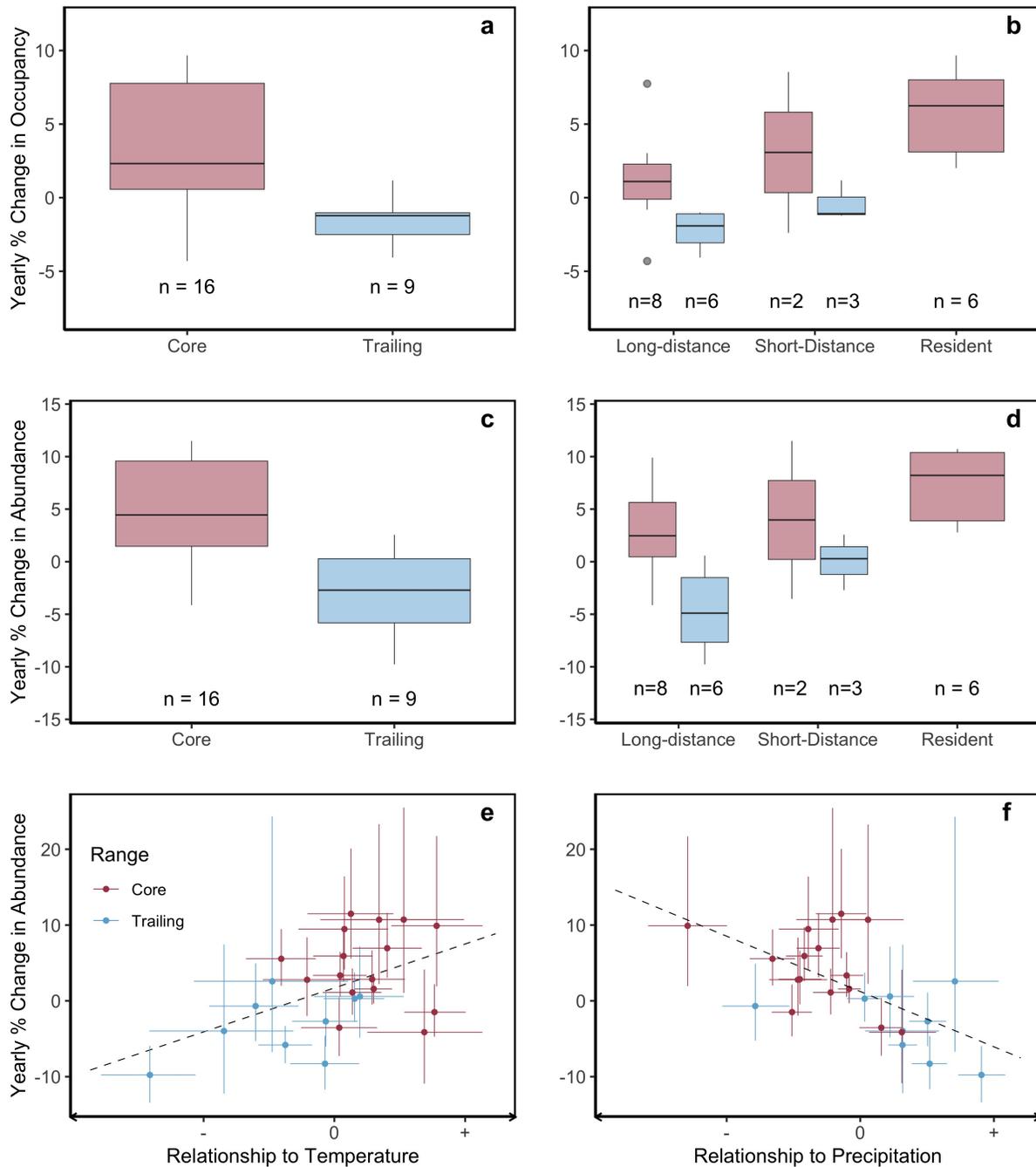


Figure 4: Average percent yearly change in abundance and occupancy from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA with species grouped by range position (a and c), migratory strategy (b and d), relationship to temperature (e) and relationship to precipitation (f). For all panels, trailing-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). Scatterplots display posterior means (points) with 95% credible intervals, while boxplots are based on posterior means for each species. The dashed lines in panels (e) and (f) display a simple linear model between coefficients and change in abundance.

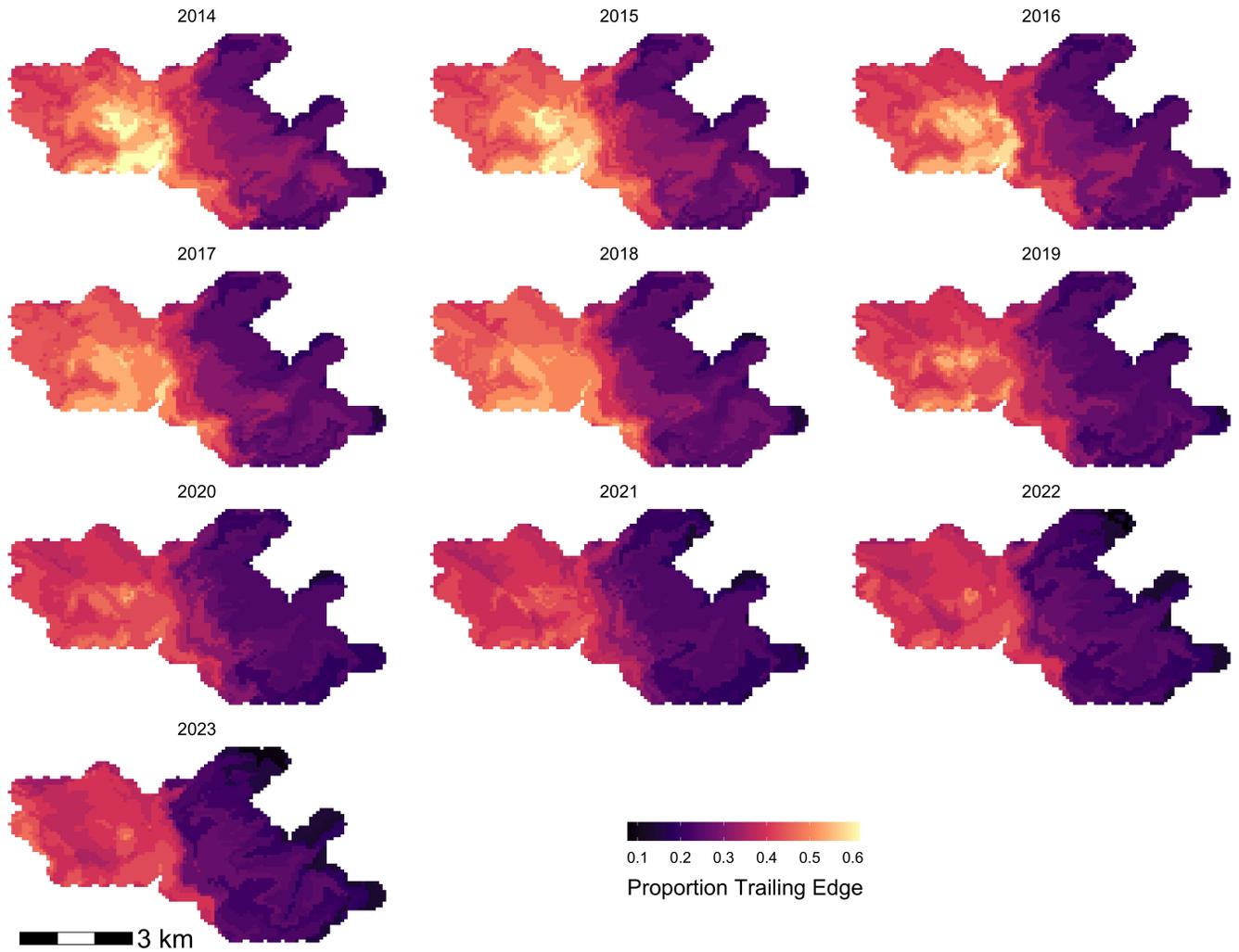


Figure 5: Proportion of species richness comprised of trailing-edge species in the Nantahala National Forest, North Carolina, USA from 2014 to 2023.

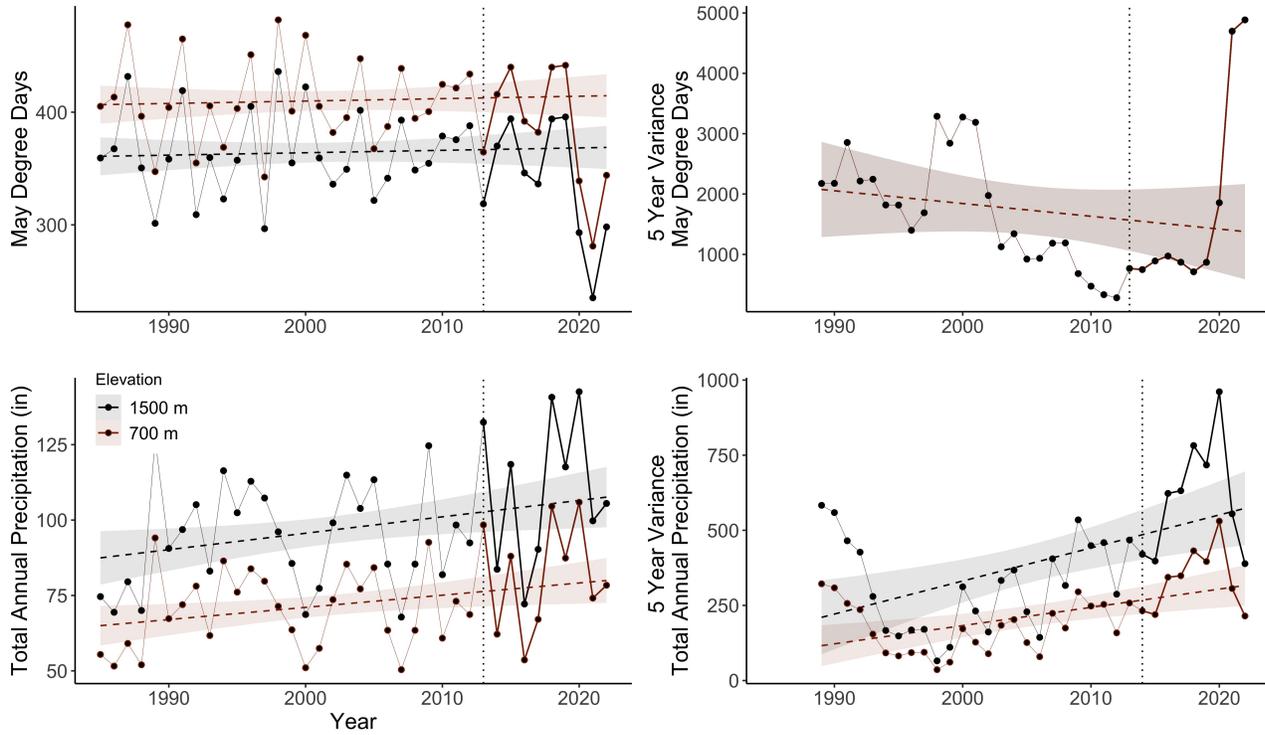


Figure S1: Temperature and precipitation conditions from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA. Trend lines from a linear model are shown with dashed lines and shaded confidence intervals. The vertical dotted line indicates the first year of the study

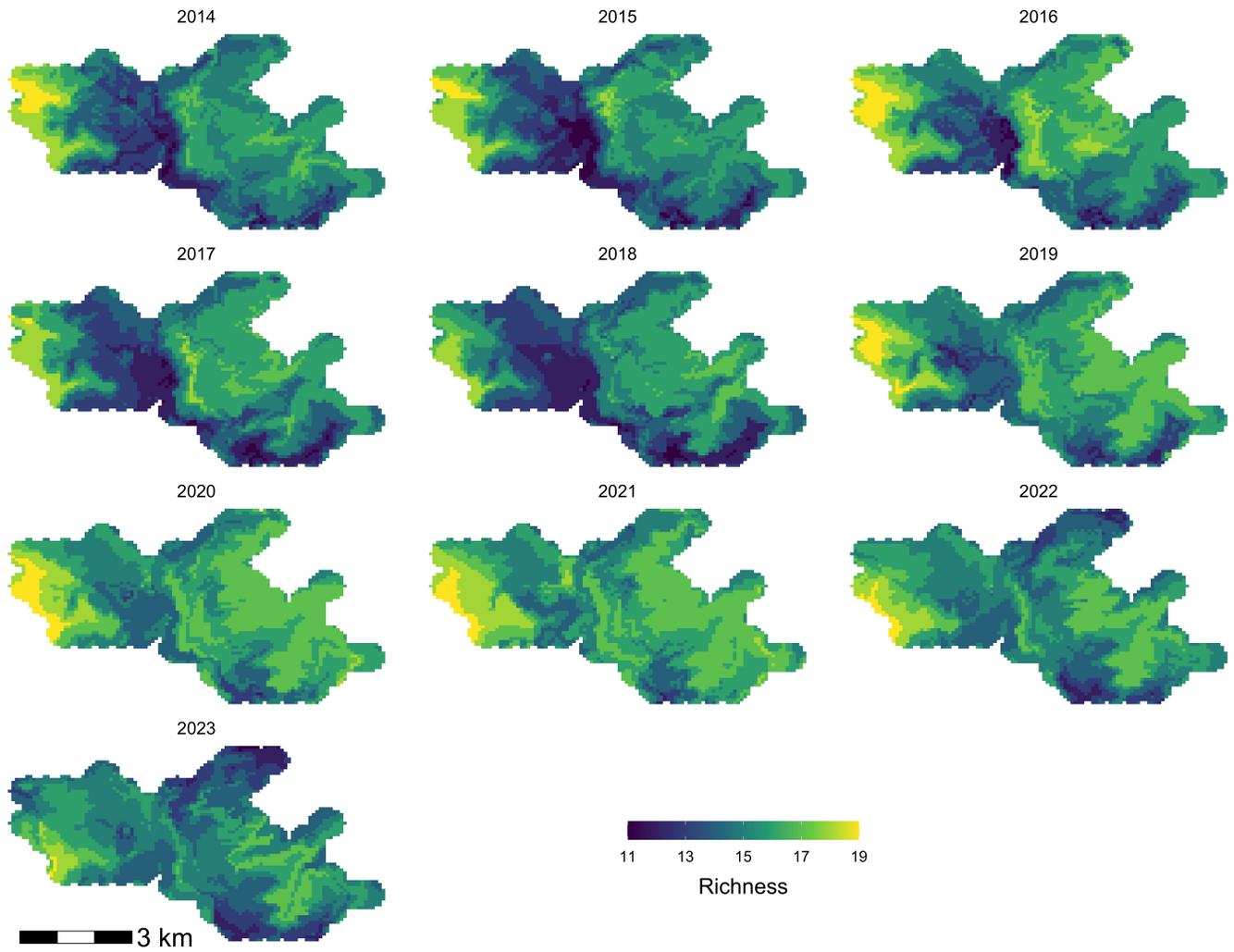


Figure S2: Spatial time-series of species richness in the Nantahala National Forest, North Carolina, USA from 2014 to 2023. Colors represent mean posterior predictions.