

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

Heather E. Gaya^{1,2} and Richard B. Chandler^{1,3}

¹ Warnell School of Forestry and Natural Resources, University of Georgia,
Athens, GA

² heather.e.gaya@gmail.com

³ rchandler@warnell.uga.edu

Running Title: Spatio-temporal community dynamics

Keywords: Abundance, Appalachian mountains, community-dynamics, climate change, elevational gradient, N-mixture, spatio-temporal dynamics, Trailing-edge

Article Type: Letter

Style: Formatted for Ecology Letters

Word Counts: Abstract - 139 words, Main text - 3423 words, References - 86, Figures - 5, Tables - 1, Text boxes - 0

Correspondence: Heather Gaya, 180 E Green St, Athens, GA 30602. heather.e.gaya@gmail.com. 1-509-703-3869

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:
<https://doi.org/10.5281/zenodo.10182963>

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; Sekercioglu *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

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 thermophilisation (Hampe & 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 species, rising temperatures could lead to increased species richness, even as trailing-edge populations decline (Lemoine & 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. 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 (Rushing *et al.*, 2020; Välimäki *et al.*, 2016; Stevens *et al.*, 2023a). 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 ground (Wittwer *et al.*, 2015; MacLean & Beissinger, 2017). Thus, extinction risk may be higher for trailing-edge populations of migratory species than resident species.

We used 10 years of avian survey data from a hotspot of trailing-edge population diversity (Merker & Chandler, 2020) in the southern Appalachian Mountains to (1) assess the generality of trailing-edge population declines, and (2) determine the consequences for community structure. We predicted species-specific shifts in abundance and occupancy would depend on range-position, migratory strategy and climate niche breadth. We predicted that cool-adapted trailing-edge 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.

2 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 & Chandler, 2020). Elevation within the region ranges from 660–1590 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 1300 m, compared to 14°C at 700 m. During the breeding season (May – July), sites above 1300 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*), birch (*Betula spp.*) maple (*Acer spp.*), fraser magnolia (*Magnolia fraseri*), and common buckeye (*Aesculus flava*). Serviceberry (*Ame- lanchier spp.*) and witchhazel (*Hamamelis virginiana*) are common in the mid-story. 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 & Swank, 2008).

Environmental Data

We calculated total annual precipitation for each year (2013–2022) based on nine 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. To represent the heat accumulation during the breeding season, we calculated growing

degree-days (Lany *et al.*, 2016; Cesaraccio *et al.*, 2001) in May of each year (2013–2022). 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 & Pearson, 2013; Lewis *et al.*, 2023). 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 0.43–33.6°C, with a mean annual precipitation of 230.6 cm.

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 hours after sunrise. Observers recorded the distance of all singing birds heard in a 10-minute session split into four consecutive 2.5-minute 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 & 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 er-

ror arising from variation in detection probability. We categorized each species by migratory 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.

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

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

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

Here again, the coefficients were modeled as random effects determined by guild structure, using the same formulation as in Eq. 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 & 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.

Species richness at site i in year t was calculated as the realized number of species present at the site: $S_{i,t} = \sum_{k=1}^K I(N_{i,k,t} > 0)$. For each location, we also calculated the proportion of richness attributable to trailing-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_k^a denote availability (probability of an individual singing during the sampling period), and let $p_{i,k,t}^d$ 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: $n_{i,k,t} \sim \text{Binomial}(N_{i,k,t}, p_k^a p_{i,k,t}^d)$, with p_k^a modeled as a random effect following a logit-normal distribution: $\text{logit}(p_k^a) \sim \text{Normal}(1, \kappa)$.

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

detection function with scale parameter δ .

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

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 MCMC iterations using three 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 & Rubin, 1992) and visual inspection.

3 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 trailing-edge of their ranges (hereafter, “trailing-edge populations”). Each core species was detected at an average of 88 sites (range 47 – 108), with a mean 43 (range 10 – 157) detections per species per year. Trailing-edge species 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 12.1–8.7 °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 (Figure S1). There was no trend in May degree days during the study period, though prior to 2020, average May temperature showed a positive trend (Lewis *et al.*, 2023).

Of the 25 species in our study, 21 species had stable or increasing populations (Figure 2). Declines were more common in trailing-edge populations than those in the core of their range (Table 1). Three trailing-edge populations declined in abundance during the study period, compared with 1 core-species. There were no trailing-edge populations with increasing abundance or occupancy (Figure 3). For species at the range core, 11 species increased in abundance, with all but 3 species (eastern towhee, eastern wood-pewee and 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 4). The largest declines in abundance were seen in long-distance migrants, with an average -0.85 % yearly change in abundance. Short-distance migrants and resident species had an average 1.4% and 7.3% yearly increase in abundance throughout the study period.

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

4 Discussion

Most models of climate change impacts on species distributions predict shifts towards higher elevations and latitudes (Walther *et al.*, 2002; Parmesan & 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 trailing-edge populations were slower than the rate of encroachment by warm-adapted populations, and thus community turnover may lag behind changes in community composition.

Continued declines of trailing-edge populations will likely result in complete reorganization of 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; Sekercioglu *et al.*, 2004). For example, in the boreal forests of North America, trailing-edge populations of seed-caching species such as Canada jays (*Perisoreus canadensis*) and boreal chickadees (*Poecile hudsonicus*) can play a critical role in oak and pine tree dispersal (Koenig & Knops, 2001; Sekercioglu *et al.*, 2004; Ralston *et al.*, 2019). Loss of trailing-edge species may also decrease genetic diversity (Harrison, 2020). Trailing-edge populations often harbor genotypes that are better adapted to climate extremes relative to populations in the core of the range (Hampe & Petit, 2005; Rehm *et al.*, 2015). Therefore the loss of locally adapted populations may not only alter local community composition, but further threaten the 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 & 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 & 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 & 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 trailing-edge species will likely transition to communities dominated by warm-adapted species.

Although trailing-edge populations declined during the ten years of investigation, none of the species in our study declined to local extinction. Thus, as warm-adapted species 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 & Didham, 2006; Urban *et al.*, 2012). However, elevated levels of species richness are usually temporary (Tilman *et al.*, 1994; Hampe & Petit, 2005; Habibzadeh *et al.*, 2021), suggesting subsequent reductions in species abundance and richness in the near future (Ewers & Didham, 2006; Halley & Pimm, 2023).

In the early years of the study, the majority of species present at high elevation sites were at the trailing-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 (Catano *et al.*, 2020; Olden & Poff, 2004), 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 trailing-edge populations continue to decline.

Climate change may also 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 already 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 & Petit, 2005; Bennett *et al.*, 2015; Robinson *et al.*, 2015), 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; Rubenstein *et al.*, 2023; Freeman *et al.*, 2018a). 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 is strongly species and region specific (La Sorte & Jetz, 2012; Thompson & 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 & 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 & King, 2014; Hovick *et al.*, 2016). Research on migratory strategies has been mixed, with some studies

demonstrating no difference between migratory strategies (Sekercioglu, 2007; Angert *et al.*, 2011; Hovick *et al.*, 2016), while others have noted significantly reduced range expansion in long-distance migrants (Laaksonen & Lehikoinen, 2013; Rushing *et al.*, 2020). We found migratory status was a poor 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 trailing-edge species had a negative relationship with temperature, while the reverse was true for range-core species. These results suggest that individual populations' range position (trailing 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.*, 2023), 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 inter-annual changes in abundance.

Although trailing-edge populations continued to persist after encroachment by warm-adapted species, 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 & Eckert, 2014). In contrast, if uphill movements represent an 'escalator to extinction' as survival and reproductive rates decline (Sekercioglu *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.

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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)*
Trailing	Wood Thrush	<i>Hylocichla mustelina</i>	WOTH	Long-distance	-0.01 (-0.05 – 0.02)
	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)

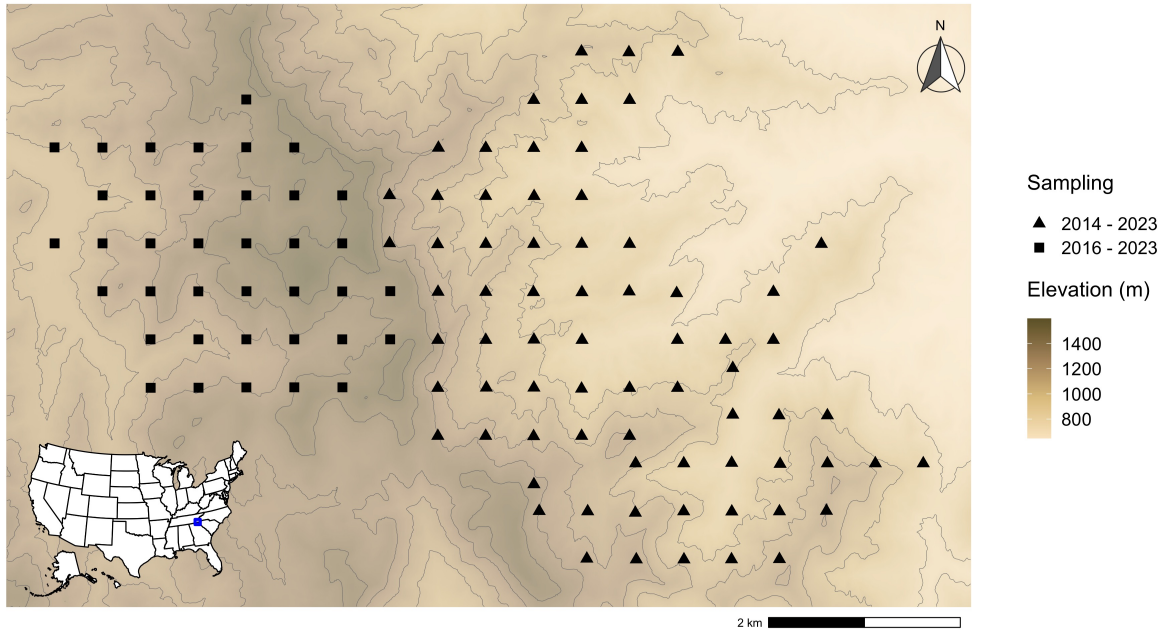


Figure 1: Map of point count locations in the Nantahala National Forest, North Carolina, USA. Points shown as triangles (right side) were surveyed from 2014-2023. Locations shown as squares (left side) were surveyed starting in 2016.

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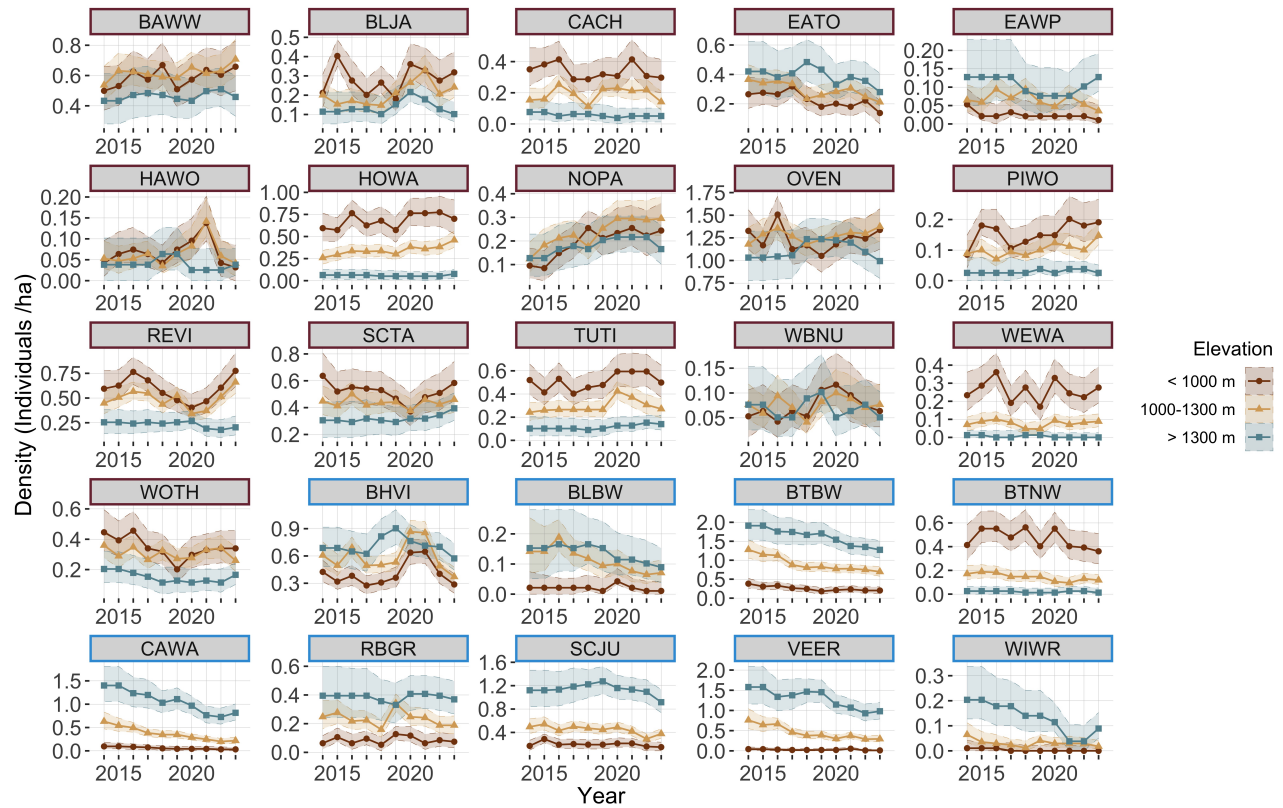


Figure 2: Temporal trends in population density at high, medium and low elevations. Estimates are the realized values of density averaged across sites within each elevation category. Point estimates are posterior means with 95% CIs. Species are sorted by range position. Headings for populations at the 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.

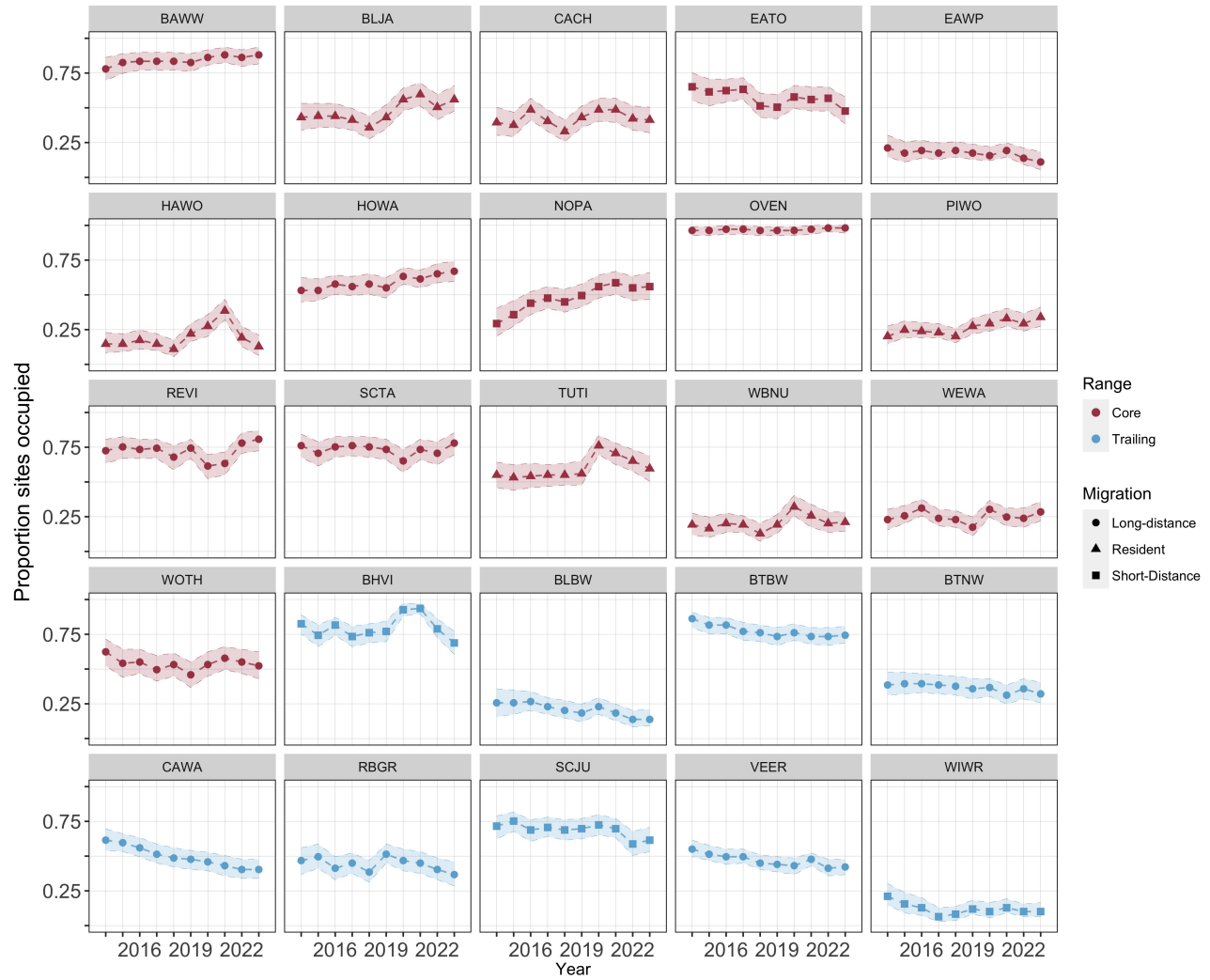


Figure 3: Site occupancy for species in the Nantahala National Forest, North Carolina, USA from 2014 to 2023. Estimates are posterior means (points) and 95% CIs. Species are sorted by range position with trailing-edge species in blue and core species in red. Point shapes indicate if a species is a long-distance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

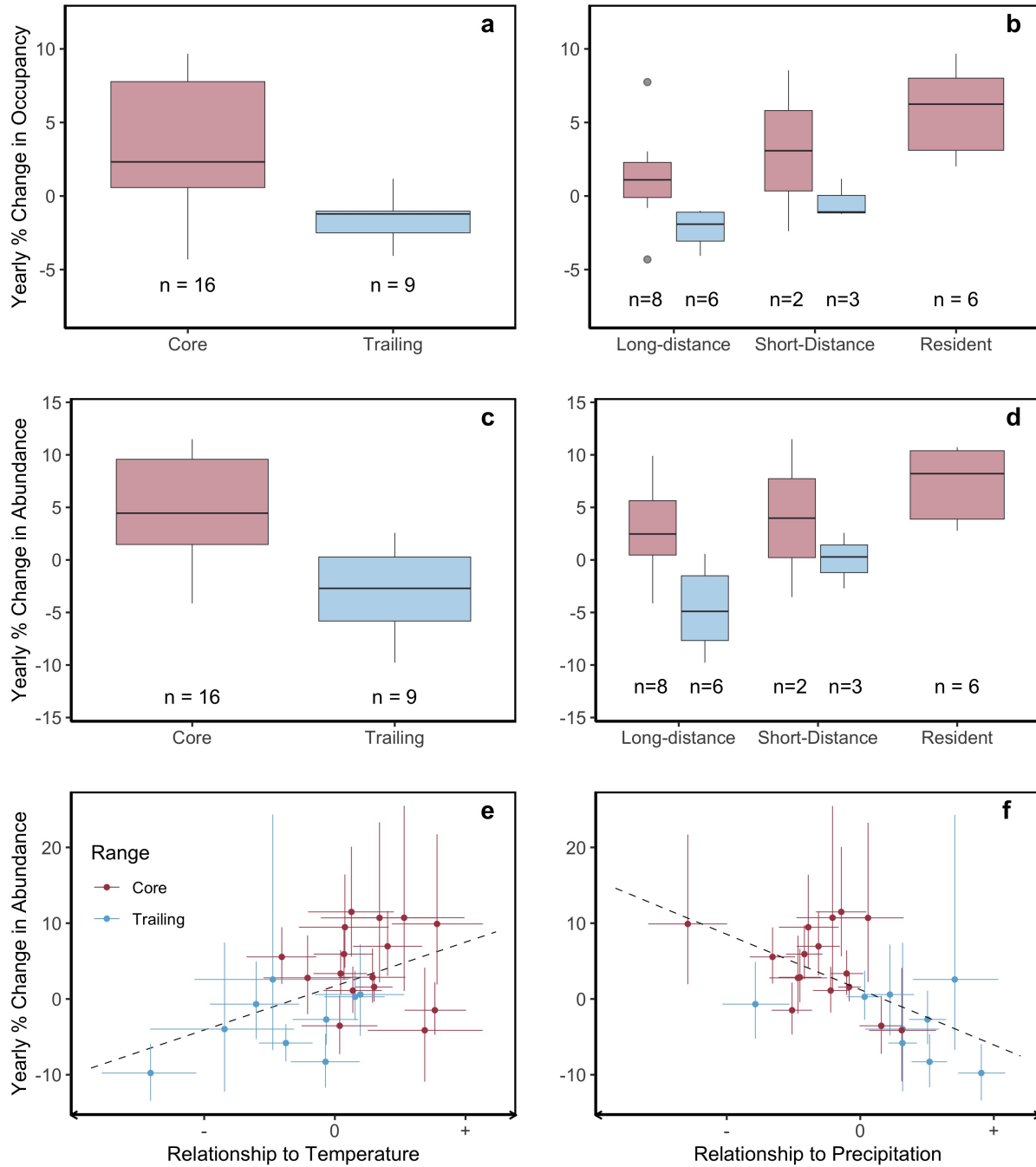


Figure 4: Average percent yearly change in abundance and occupancy from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA with species grouped by range position (a and c), migratory strategy (b and d), relationship to temperature (e) and relationship to precipitation (f). For all panels, 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.

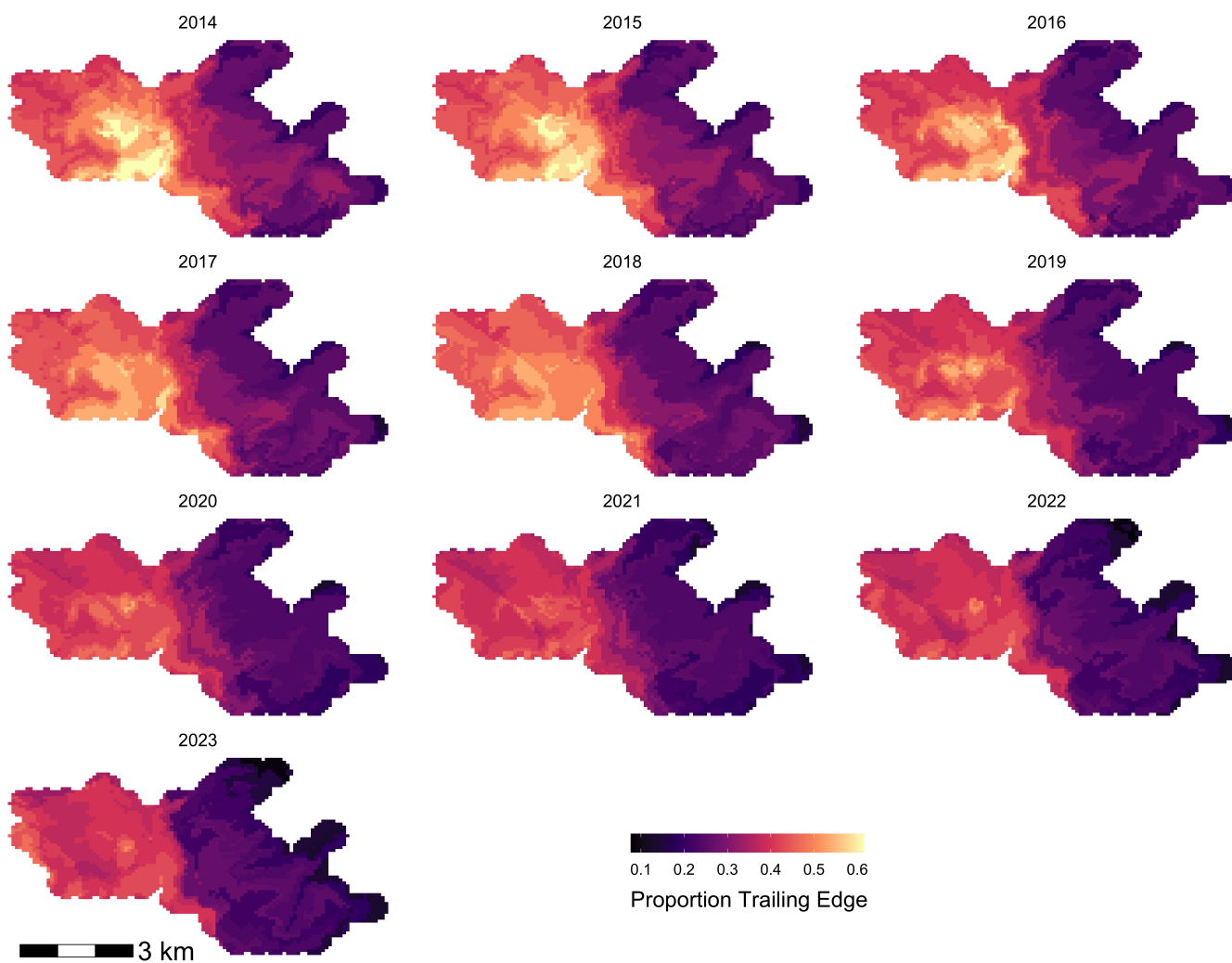


Figure 5: Proportion of species richness comprised of trailing-edge species in the Nantahala National Forest, North Carolina, USA from 2014 to 2023.

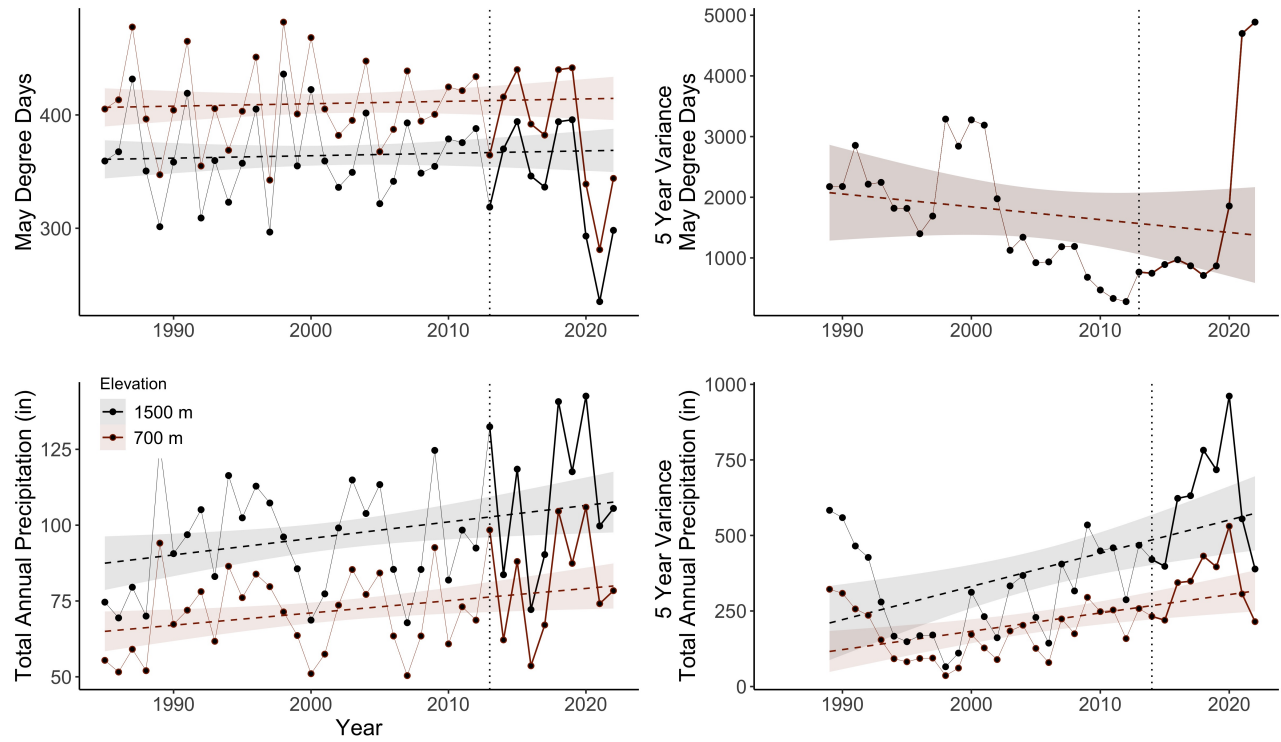


Figure S1: Temperature and precipitation conditions from 2014 to 2023 in the Nantahala National Forest, North Carolina, USA. Trend lines from a linear model are shown with dashed lines and shaded confidence intervals. The vertical dotted line indicates the first year of the study

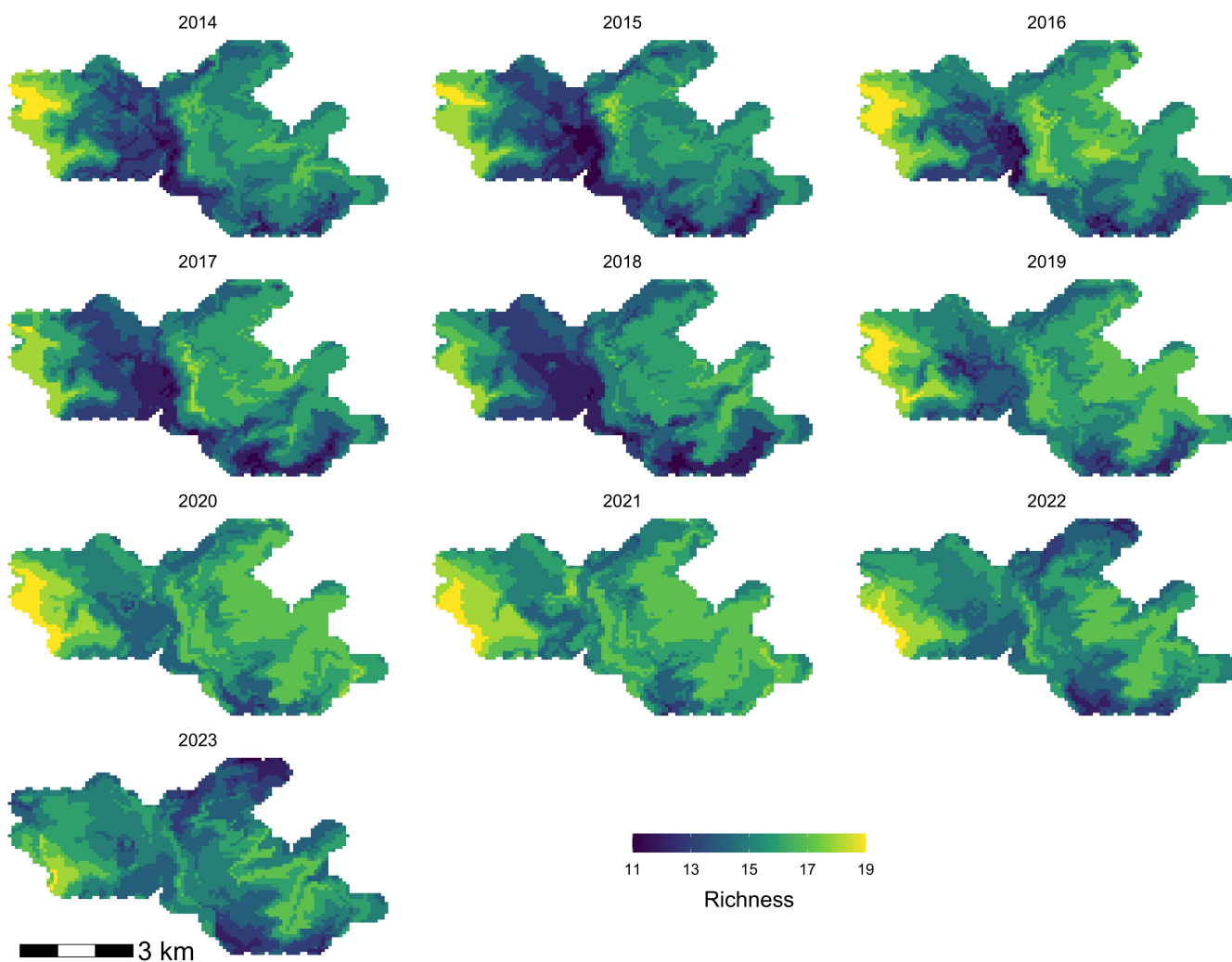


Figure S2: Spatial time-series of species richness in the Nantahala National Forest, North Carolina, USA from 2014 to 2023. Colors represent mean posterior predictions.