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The Relationship between Grinnellian and Eltonian Niche Characteristics and Passerine Distribution across a Latitudinal Gradient

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Abstract: The degree to which Grinnellian and Eltonian niche characteristics influence species distribution may depend on latitude. Tropical regions are environmentally stable and resource-rich, whereas temperate regions are comparatively less environmentally stable (e.g., environmental filtering). Moreover, phylogenetic niche conservatism could influence distributions by inhibiting the ability for species to colonize environmentally different locations. Herein, we examine relationships between niche characteristics, passerine distributions, and phylogenetic niche conservatism across the latitudinal gradient. We used environmental and climatic variables to characterize Grinnellian niches and diets to characterize Eltonian niches. We conducted variation partitioning with retained components from ordination methods to evaluate the degree of association of Grinnellian and Eltonian niche characteristics with passerine distribution across latitudes. We examined the relationship between phylogenetic signal and niche characteristics with a phylogenetic regression. Passerine distributions were more related to environmental gradients than resources across latitudes. While niche conservatism was prevalent in Eltonian niche characteristics, phylogeny was related to Grinnellian niche characteristics in only 46% of biomes. There was no latitudinal gradient in phylogenetic niche conservatism or the degree to which Eltonian and Grinnellian niche characteristics relate to passerine distribution. Niche conservatism, albeit weak, was present for Grinnellian niche characteristics, thus potentially influencing the expansion of passerine distributions into the northern hemisphere.

Keywords: avian; conditions; neotropical; resources; phylogenetic niche conservatism



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1. Introduction

Geographic distributions are influenced by a multitude of factors, such as dispersal ability and ecological niche characteristics [1]. The ecological niche has become a foundational concept in population and community ecology [1,2]. However, the concept has become hard to define due to its multiple meanings. Soberón suggested separating ecological niche characteristics into two different kinds that reflect the concepts introduced by Grinnell and Elton [1,3,4]. The Grinnellian niche can be defined as the set of environmental conditions that allow a species to persist in a particular area [3]. The Eltonian niche can be defined as the biotic interactions, resources, and consumer dynamics that allow for the coexistence of species within communities [4]. Conceptually, the effects of Grinnellian and Eltonian niche characteristics on distribution of species operate at different spatial scales, whereby Grinnellian niche characteristics encompass climatic and landscape gradients across coarse spatial scales, and Eltonian niche characteristics involve biotic interactions at the local level [1].

The degree to which Eltonian and Grinnellian niche characteristics relate to the distribution of species may vary across a latitudinal gradient (e.g., tropical vs. temperate

regions). Eltonian niche characteristics in the tropics may be stronger drivers of distribution of species due to the presence of stronger biotic interactions [5] and greater resource availability [6]. Speciation driven by biotic interactions, such as interspecific competition, is one mechanism proposed to explain the latitudinal gradient in species richness (competition hypothesis) [5,7]. In climatically stable environments, species may more readily reach carrying capacity, and this may increase the intensity of interspecific competition and cause species to partition resources or segregate into areas in which they are best adapted [7]. Intense interspecific competition in areas with high habitat heterogeneity also allows spatial niche partitioning and specialization [7]. Thus, it has been hypothesized that competition can drive natural selection in the tropics, therefore leading to narrower niches and greater diversity [8].

The debate surrounding a latitudinal gradient in biotic interactions has had mixed responses. Many studies have demonstrated a latitudinal gradient in the strength of predation, herbivory, and parasitism [9–11], whereas many other studies question the idea [12–14]. There has been a push to move beyond this idea and create more insightful ecological theories [15]. However, some studies continue to suggest that biotic interactions influence community structure along elevational gradients in the tropics [16–19]. Sherry et al. [19] suggested that the evidence of specialization in tropical insectivorous birds may inject life back into the idea of radiation and biotic interactions in the tropics. Whether or not there should be a continuation of ecological studies centering around a latitudinal gradient in biotic interactions remains contentious. However, research focusing on the relationship between Eltonian niche characteristics and species distribution may contribute to the context of a better understanding of latitudinal gradients of biodiversity.

Environmental filtering in temperate areas may play a more critical role in natural selection than biotic interactions such as competition [7,20]. Communities in areas with unpredictable and harsh abiotic conditions often have lower diversity [21]. Furthermore, resource availability is often highly correlated with primary productivity [6]. For example, tropical regions have a greater diversity of insects and plant species, thus potentially giving rise to higher diversification rates of passerines [6]. Increased actual evapotranspiration, a simple surrogate for primary productivity, was highly associated with frugivore and insectivore richness [6]. Therefore, the degree to which community structure is influenced by climatic variation or biotic interactions may be represented by a gradient from polar to tropical regions [21].

Niche conservatism also has the potential to influence the distributions of species. Niche conservatism is the tendency for species to retain ancestral niche characteristics [22]. The tropical niche conservatism concept has been used to explain the accumulation of diversity at lower latitudes [23]. Species that diversify at lower latitudes may be unable to expand their distributions to higher latitudes due to retaining ancestral climate tolerances [24,25]. Therefore, species are predicted to occupy environments similar to those near their origin, thus slowly expanding outward to more novel habitats [24,25]. Climatic tolerances that are inherited from an ancestor and competition among already established species may slow the expansion of geographic distributions [26].

The order Passeriformes (perching birds) makes an ideal clade to measure niche conservatism and the relationship between different niche concepts and distribution across the latitudinal gradient. Passerines comprise 60% of extant birds [27,28], approximately 6400 species and 141 families [29]. Researchers have proposed that most New World passerines (specifically the clade Passeri) originated in Gondwana [30,31] approximately 50 million years ago [32]. Passerines immigrated into the tropics, which stimulated radiation and allowed families to diversify [33,34]. Many passerine groups moved northward and colonized North America approximately 25 to 30 million years ago [35].

Herein, we compared the relative contributions of Grinnellian and Eltonian niches to passerine distributions and the phylogenetic relatedness of niches across different biomes of the western hemisphere. Because Eltonian and Grinnellian niches describe resource–consumer dynamics and environmental tolerances, respectively, we predict that both niche concepts will account for significant variation in passerine distributions across all biomes. Second, if there is a latitudinal gradient in biotic interactions and resource availability, we predict that the relationship between Eltonian niche characteristics and distribution will be stronger at lower latitudes than for Grinnellian niche characteristics. If passerines exhibit more niche conservatism related to the latitudinal gradient in diversity, we predict that species in tropical biomes will do so for both their Grinnellian and Eltonian niches, whereas a phylogenetic signal related to niche conservatism will not be significant in temperate biomes. We evaluated this prediction by measuring the relationship between Eltonian and Grinnellian niche characteristics with phylogenetic signals related to niche conservatism for each biome.

2. Materials and Methods

2.1. Biomes

We compared information from biomes to examine the relationship between passerine distribution and niche characteristics across latitudinal gradients. To collect distribution information for each biome, we created a 5 km-by-5 km grid. We used biomes characterized by Olson et al. [36], who divided the world into 8 biogeographical realms and 14 types of biomes by modifying the systems of Dinerstein et al. [37] and Ricketts et al. [38]. Characterization of biomes was dependent on major vegetation types and predominant climatic conditions in each primary habitat type. The Nearctic realm contained 10 distinct biomes, whereas the Neotropical realm contained 11 distinct biomes. Due to their geographical separation, we divided a few biomes into independent study areas due to being separated by more than 800 km. Even though biomes have the same classification, the geographical separation can lead to a difference in ecological factors (e.g., actual evapotranspiration, elevation, human impact, climate; Table 1), which will impact community composition. There was a noticeable difference in species richness (more than 70 species) across similar yet spatially separated biomes (Table 1). We divided Nearctic temperate conifer and broadleaf forests biomes into east and west (Table 1). We divided Neotropical desert and xeric shrublands and tropical and subtropical dry broadleaf forests into north, east, and west (Table 1). We divided tropical and subtropical grasslands into north and south (Table 1).

The Neotropical realm has three geographically separated flooded grassland and savanna areas. However, we removed the Orinoco wetlands in Venezuela and Guayaquil-flooded grasslands in Ecuador due to insufficient data. The Orinoco wetlands and Guayaquil flooded grasslands have areas of 60,906 and 2924 km², respectively. We had no recorded species for the Orinoco wetlands and 24 species across three sites in Guayaquil flooded grasslands. With so few sites and species, we removed the Guayaquil flooded grasslands from our analyses, since we could not properly analyze the relationship between niche characteristics and passerine distributions. Therefore, 28 biomes were used in this study: 12 in the Nearctic and 16 in the Neotropical realms (Table 1).

Table 1. Descriptive information for each biome and location across the latitudinal gradient. Biomes and numbers (Biome #) associated with them were established by Olson et al. [36]. Area was collected from Olson et al. [36] data; average AET, elevation, human index, precipitation, maximum and minimum temperature were gathered from rasters in ArcGIS. Latitude and longitude are the centroid for each biome. Biomes are listed from northern pole to southern pole. R = species richness, AET = actual evapotranspiration, Human = human index, Precip = precipitation, T_{\max} = max temperature, T_{\min} = Temperature minimum.

	#	Nearctic Biomes	R	Area (km ²)	AET (mm)	Elevation (m)	Human (0–1)	Precip (mm)	T_{\max} (°C)	T_{\min} (°C)	Latitude	Longitude
Northern Hemisphere	11	Tundra	87	271,663,882	3645.00	386.76	0.02	33.54	8.17	0.49	67.40466	−110.99
	6	Boreal Forests	140	49,903,944	7152.00	398.45	0.04	65.43	17.16	5.47	57.80348	−103.865
	5 west	West Temperate Conifer Forests	224	23,759,410	8321.00	1384.91	0.14	52.98	20.23	5.36	48.19165	−119.473
	4 west	Temperate Broadleaf & Mixed Forests	78	14,883	8120	142.74267	0.63	31.96	25.54	10.05	44.86379	−122.981
	8	Temperate Grasslands, Savannas & Shrublands	245	4,734,502	9357.00	669.08	0.32	65.58	27.36	12.02	43.77383	−102.673
	4 east	Temperate Broadleaf & Mixed Forests	189	25,307,930	10,211.83	279.43679	0.58	125.1	25.21	13.76	41.34244	−82.5103
	12	Mediterranean Forests, Woodlands & Scrub	157	423,811	5768.00	594.52	0.35	6.11	29.41	13.18	35.52935	−119.397
	5 east	East Temperate Conifer Forests	151	9,064,846	13,177.00	45.65	0.33	181.51	30.78	19.79	32.20068	−84.9705
	13	Deserts & Xeric Shrublands	271	10,865,373	5418.00	1311.73	0.23	29.39	31.3	13.95	34.2914	−109.93
	2	Tropical & Subtropical Dry Broadleaf Forests	77	356,321	9062.00	402.36	0.22	99.67	36.78	20.97	28.12188	−109.692
	7	Tropical & Subtropical Grasslands, Savannas & Shrublands	152	2,334,935	12,462.00	12.34	0.34	146.93	32.04	22.6	29.03471	−94.5135
	3	Tropical & Subtropical Coniferous Forests	226	31,426,924	9549.00	1882.62	0.15	103.11	29.22	13.44	26.03234	−105.109
	Neotropic Biomes											
Equator	3	Tropical & Subtropical Coniferous Forests	326	12,001,989	10,777.72	1457.58	0.25	219.04	27.66	16.13	17.02859	−94.3459
	13 north	North Deserts & Xeric Shrublands	222	271,032	10,068.95	391.8	0.31	132.91	31.41	21.67	11.40241	−72.2085
	2 north	North Tropical & Subtropical Dry Broadleaf Forests	388	2,847,807	883.96	510.29	0.28	165.03	32.11	20.61	13.39755	−89.0349
	7 north	North Tropical & Subtropical Grasslands, Savannas & Shrublands	168	3,217,561	848.86	187.98	0.21	271.91	31.02	22.62	5.93031	−66.2061
	14	Mangroves	282	7,916,251	11,567.51	12.25	0.22	178.43	31.68	22.86	3.416023	−64.7089
	1	Tropical & Subtropical Moist Broadleaf Forests	862	119,022,002	9899.31	400.29	0.13	141.86	29.88	19.28	−4.932322	−63.0036
	13 east	East Deserts & Xeric Shrublands	155	2,925,280	5676.83	422.87	0.26	29.58	28.9	18.37	−8.639252	−39.8674
Southern Hemisphere	2 east	Southeast Tropical & Subtropical Dry Broadleaf Forests	92	1,198,761	798.85	547.18	0.24	133.41	31.01	19.51	−12.49221	−43.2687
	9	Flooded Grasslands & Savannas	163	2,274,986	7117.79	104.72	0.16	66.54	28.21	16.64	−21.55915	−57.5349
	10	Montane Grasslands & Shrublands	223	6,005,435	1293.01	3619.09	0.21	12.62	12.42	−3.41	−21.80844	−69.0883
	13 west	West Deserts & Xeric Shrublands	98	289,116	819.98	1803.8	0.22	1.21	20.02	7.05	−16.65466	−73.0378
	7 south	South Tropical & Subtropical Grasslands, Savannas & Shrublands	375	62,827,392	730.84	382.57	0.21	170.99	31.16	19.58	−20.16100	−54.6077
	2 west	Southwest Tropical & Subtropical Dry Broadleaf Forests	175	1,031,940	1011.18	857.86	0.17	167.21	29.65	19.05	−16.83261	−61.6999
	12	Mediterranean Forests, Woodlands & Scrub	55	148,381	1380.01	981.99	0.27	61.29	14.49	4.83	−31.15619	−71.0188
8	Temperate Grasslands, Savannas & Shrublands	164	6,659,747	1560.23	395.4	0.23	33.69	13.53	2.64	−39.72482	−39.7248	
4	Temperate Broadleaf & Mixed Forests	67	37,615,866	1225.11	646.3	0.13	163.97	7.08	0.22	−45.35145	−72.0871	

2.2. eBird Data

Climatic conditions and resource availability, which are reflected by Grinnellian and Eltonian niches, respectively, are seasonally dependent and drive the seasonality of many bird communities [39,40]. A good example of conditions and resources influencing avian behavior occurs during the breeding season. Avian breeding seasons depend on external factors, such as temperature and food availability, that can trigger gonadal enlargement [41]. The decreased variability in climatic conditions in the tropics allows birds to have longer breeding seasons [41]. Furthermore, climatic conditions synchronize with photoperiod [42], which can have a greater effect on avian reproductive response [43]. In the tropics, photoperiod is less variable than toward the poles [44]. To decrease the potential influence of seasonality, we obtained eBird occurrence records north of the equator from May to August 2017 and occurrence records south of the equator from November 2017 to February 2018. From May to August, many temperate migrants from the southern hemisphere arrive at their northern temperate breeding areas [45]. In Costa Rica and Guatemala, the breeding season for many birds is ongoing, with peak months from April to June [46]. The breeding season corresponds to high resource availability due to rainfall [46]. May has the heaviest rainfall in Costa Rica [46,47]. Rainfall decreases into June and August, but rainfall does not drop below 250 mm per month [46,47]. In the temperate regions in the southern portion of South America, June to August are the coldest months of the year; depending on the species, breeding there occurs between October to February [48]. Therefore, distributions of species related to climatic conditions and resource availability may differ from their breeding season.

In 2002, the Cornell Lab of Ornithology and National Audubon Society launched eBird as a large-scale citizen science-based network to gather bird data. Individuals upload checklists of avian observations, which are then vetted. This information can be used for numerous types of studies, such as those on distribution of species, abundance, migration timing, and conservation tactics [49]. eBird consists of data covering large geographical areas and long-term monitoring. Therefore, eBird is useful because researchers alone cannot achieve such extensive surveys. However, there are biases when using eBird, such as false absences, lack of detection of cryptic species, different levels of expertise of contributors, no standardized protocols, and spatial and temporal biases, among others [49]. eBird tries to minimize the effect of these biases by monitoring each observation and increasing communication between observer and expert [49,50]. We implemented filters for the downloaded data to further improve quality and detection probabilities. First, we used only complete checklists to avoid false absences or preferences toward one species. Second, we used stationary and traveling protocols where the observer traveled less than 2.5 km, thereby decreasing spatial bias. To reduce temporal bias and increase effort, we kept checklists where the observer spent 5 to 240 min making observations. We removed duplicate checklists made by groups of individuals participating in recording eBird observations at the same location and time. These methods are similar to those recommended by Callaghan et al. [51,52] and Johnston et al. [53]. Adding these filters has improved models [53] and increased detection effort over large spatial scales [54].

To examine passerine distribution in each biome, we created 5 km-by-5 km cells (from now on, sites) using the fishnet tool in ArcMap 10.7.1 [55]. We plotted avian observations and extracted the locations within the grid for each biome. This provided information on what species were recorded in which 5km-by-5 km site. Then, we created a species-by-site (presence/absence) matrix for each biome.

2.3. Grinnellian Niche

For Grinnellian niche characteristics, we collected information on actual evapotranspiration [56], human footprint [57], elevation [58], and maximum and minimum temperature and precipitation [59] for the sites that had an eBird observation. Elevation, AET, human footprint, and climatic information can greatly influence species distributions, as well as provide valuable information on Grinnellian niche characteristics. Elevational diversity gra-

dients can influence species distribution due to changes in rainfall, productivity, resources, temperature, and area [60–64]. Actual evapotranspiration measures water removed via transpiration or evaporation and is a useful indicator of primary productivity [65]. Actual evapotranspiration is an important indicator of avian range size [28] and richness at global scales [66]. Humans have altered primary productivity, increased pollution, buffered seasonal variation, and influenced community dynamics [67].

In addition to providing valuable insights into Grinnellian niche characteristics, there exists a substantial volume of data on AET, elevation, human index, and climate capable of encompassing the entirety of the Western Hemisphere. Data on global actual evapotranspiration was collected from 2017 at a resolution of 1 km² [56]. Keys et al. [57] created a machine-learning program that collects Landsat imagery from 2019, examines human development, and then creates a human footprint index at a global scale (resolution: 1 km²). We obtained elevation images from USGS, and we stitched the images together in ArcMap (resolution: 1 km²). We collected maximum temperature, minimum temperature and precipitation for May to August 2017 north of the equator and November 2017 to February 2018 south of the equator from WorldClim [59]. In ArcMap, we independently averaged precipitation and maximum and minimum temperature rasters across months. We used the resample tool in ArcMap to change the resolution of the climatic rasters from 16 km² to 1 km².

We calculated mean, maximum, and minimum values for each environmental condition for each raster with zonal statistics in ArcMap 10.7.1 across all 25 km² sites. Using similar techniques developed by Stevens [68], we calculated the maximum, minimum, and mean conditions for each species across the sites.

2.4. Eltonian Niche

For Eltonian niche characteristics, we collected dietary information from Eltonian Traits 1.0 [69]. Wilman et al. [69] collected dietary, foraging, and morphological information for 9993 extant bird species. For dietary information, they translated dietary components into proportions (0 to 100) to represent principal dietary items. They created nine dietary categories ranging from invertebrates to seeds. With this information, we created a matrix of species by dietary categories for each species for each biome.

2.5. Statistical Analyses

To examine the relationship between distributions of species and their niche characteristics, we created a species (rows) by sites (columns) matrix for each biome (similar to the methods of Stevens [68]). For most biomes, the species-by-site matrix was wide. A wide matrix has linearly dependent columns [70]. To avoid this issue when conducting constrained analyses, we conducted individual correspondence analyses (CAs) on the species-by-site matrix for each biome to decrease the number of columns. Correspondence analysis is typically used for species-by-site matrices that are zero-inflated. However, because CA uses a chi-square metric, it gives higher weight to rare species (in this case, sites) [71]. To decrease the weight of sites in a CA, we followed methods suggested by McGarigal et al. [72] for removing rare species. Whereas McGarigal et al. [72] suggest removing species occurring at less than 5% of sites, we removed sites that contained less than 5% of species. Most sites that we removed had only one species occupying them.

We conducted CAs with the package *ade4* [73] in R 4.3.3 [74] on all species by site matrices across the different biomes. We used the elbow technique as a stopping rule to determine how many vectors to retain [75]. The elbow technique consists of plotting explained variations of the new derived components and determining where the inflection point (elbow) is on the scree plot. We used dimensions before the elbow in subsequent analyses [75].

We conducted principal components analyses (PCAs) on Grinnellian niche characteristics and Eltonian niche characteristics for each biome. We converted the data for the Eltonian niche matrix based on a Hellinger transformation. Principal components anal-

yses were conducted in package *vegan* [76] in R 4.3.3 [74], and we used the broken stick criterion [77] to determine the number of PCs to retain. From that point forward, we used significant PCs of Eltonian and Grinnellian niche characteristics in analyses.

We determined Principal Coordinate of Neighbor Matrices (PCNMs) for each biome to account for underlying spatial structure that may influence the results of our study [78]. A PCNM analysis creates newly derived variables from site coordinates [78]. The new variables represent spatial structure from coarse to fine scales. To construct PCNMs for our dataset, we calculated the centroid for *x* and *y* coordinates for each species within each biome. Following methods suggested by Borcard and Legendre [78] and Borcard et al. [79], we calculated the distance with Euclidean distance and constructed PCNMs with the function “*pcnm*” in package *vegan* [76] in R 4.3.3 [74]. Next, we conducted a Redundancy Analysis (RDA) with those PCNMs with positive eigenvalues and detrended data from the species-by-site matrix. We determined PCNMs with forward selection with an adjusted R^2 threshold. Significant PCNMs were used in subsequent analyses.

We conducted variation partitioning with an RDA to remove spatial structure and examine the relationship between Eltonian and Grinnellian niche characteristics and distribution of species. Variation partitioning examines the relationship between independent variables (spatial structure, Grinnellian and Eltonian niche characteristics) and dependent variables (distribution of species). We can examine the unique contributions of Grinnellian and Eltonian niche characteristics and species distribution by removing the influence of spatial structure. Redundancy analyses were conducted in Canoco 5 [80] with 499 Monte Carlo permutations to determine the significance of the multivariate relationships. We conducted RDAs for each biome.

We collected 5000 phylogenetic trees for our focal species based on the backbone of Hackett et al. [81] from *birdtree.org* [82] to examine the relationship between phylogenetic structure and species Grinnellian and Eltonian niche characteristics. We followed methods of Abeyrama and Seneviratne [83] and Olalla-Tárraga et al. [28]. We created a consensus tree using “*TreeAnnotator v1.10.4*” with the software BEAST [84]. For the consensus tree parameters, we set the first 100 trees to be burn-ins, set the posterior probability to 0.75, set the tree type to “Maximum clade credibility tree”, and set the median node height of the posterior distribution.

We used the consensus tree to examine the relationship between phylogenetic inertia and niche characteristics and created a phylogenetic distance matrix with square root transformation for species in each biome [85]. We created distance matrices with package *ape* [86] in R 4.3.3 [74]. We conducted principal coordinates analysis for each distance matrix. We determined the number of derived axes to retain with the broken stick criterion [77]. Next, we conducted RDAs on significant PCs of Eltonian and Grinnellian niche characteristics (dependent variables) separately and using significant principal coordinate analysis (PCoA) axes from phylogenetic information for each biome. We centered and standardized response data to avoid singularity issues.

To examine the degree to which Eltonian and Grinnellian niche characteristics relate to species distribution across a latitudinal and longitudinal gradient, we conducted a Spearman’s rank correlation with unique variation accounted for by Grinnellian and Eltonian niche characteristics from the redundancy analyses and absolute value of latitude and longitude. We expected a significant negative correlation between importance of (R^2) Eltonian niche characteristics and latitude, whereas we expected a positive correlation between importance of Grinnellian niche characteristics and the latitudinal gradient. Next, we conducted correlation analyses on variation accounted for by phylogenetic structure on Grinnellian and Eltonian niche characteristics and the absolute value of latitude from each biome. Our critical values were 0.361 and -0.361 for each correlation analysis. We conducted Spearman correlations in R 4.3.3 [74].

3. Results

3.1. Distribution

Correspondence analyses conducted on species presence/absence for each of the biomes yielded between one and nine dimensions with the elbow technique (Table 2). Retained dimensions accounted for 12.16% to 46.29% of the variation among species regarding distribution (Table 2). The first two axes of avian distributions often reflected gradients spanning from north to south (latitudinally) or east to west (longitudinally, Figure S1). It was difficult to interpret CA-2 for the Neotropical temperate grasslands, savannas, and shrublands (Figure S1). A Pearson correlation analysis indicated a strong association between the CA-2 and minimum temperature where species were present ($r = -0.24$, $p = 0.002$).

Table 2. Correspondence analyses (CAs) were on passerine presence throughout biomes in the western hemisphere. Retained axes from CAs were determined using the elbow technique. Principal Coordinates of Neighboring Matrices (PCNMs) were conducted on x and y centroids for passerine distributions for each biome to examine coarse to fine spatial patterns. Redundancy analyses were conducted on detrended species presence data and PCNMs. We determined which PCNMs to re-train using forward selection with adjusted R^2 threshold to account for the number of explanatory variables. Biome number: 1 = Tropical and Subtropical Moist Broadleaf Forests, 2 = Tropical and Subtropical Dry Broadleaf Forests, 3 = Tropical and Subtropical Coniferous Forests, 4 = Temperate Broadleaf and Mixed Forests, 5 = Temperate Conifer Forests, 6 = Boreal Forests, 7 = Tropical and Subtropical Grasslands, Savannas and Shrublands, 8 = Temperate Grasslands, Savannas and Shrublands, 9 = Flooded Grasslands and Savannas, 10 = Montane Grasslands and Shrublands, 11 = Tundra, 12 = Mediterranean Forests, Woodlands and Scrub, 13 = Deserts and Xeric Shrublands, 14 = Mangroves. For CAs, % = total percent variation explained by components. For PCNMs, % variation represents adjusted variation calculated during RDA with forward selection.

#	Distribution		PCNM	
	Axes	%	Axes	%
11	4	22.24	0	0.00
6	5	17.58	0	0.00
5 west	6	18.05	0	0.00
4 west	2	20.56	0	0.00
8	8	22.13	22	26.09
4 east	4	13.24	3	18.78
12	9	25.59	2	15.03
5 east	4	12.98	1	7.59
13	7	20.35	13	18.65
2	1	18.65	9	23.19
7	5	23.07	0	0.00
3	5	35.32	0	0.00
3	8	27.35	16	72.74
13 north	4	32.60	5	7.86
2 north	3	19.28	28	20.50
7 north	5	34.76	15	16.35
14	5	26.89	32	18.87
1	3	29.22	45	20.86
13 east	4	27.55	20	17.34
2 east	3	46.29	11	35.53
9	3	19.58	10	19.11
10	3	22.46	44	31.63
13 west	4	27.42	4	5.90
7 south	6	22.35	21	21.18
2 west	2	23.25	15	18.63
12	3	27.40	0	0.00
8	6	25.95	7	15.83
4	3	17.40	0	0.00

3.3. Eltonian Niche Characteristics

Principal components analysis on Eltonian niche characteristics yielded between one and three dimensions based on the broken stick criterion across biomes. The retained dimensions accounted for 65.32% to 84.46% of the variation in dietary characteristics (Tables 4 and S2). For most biomes, we retained two dimensions of dietary characteristics. For the first dimension, there was a gradient of species with primarily an insectivorous to granivorous diet in the Nearctic realm and southern temperate and desert biomes in the Neotropical realm (Table 4), whereas there was a gradient of species with primarily an insectivorous to frugivorous diet in the tropical region of the Neotropics (Table 4). For the second dimension, Nearctic biomes and Neotropical temperate and southern desert biomes exhibited a gradient of species that ranged from those that are primarily insectivorous to those that are primarily frugivorous, and northern Neotropical biomes exhibited a gradient of species that primarily have an insectivorous diet to those that primarily have a granivorous diet.

Table 4. First dimension of principal component analyses conducted on Eltonian niche characteristics of birds from biomes in the western hemisphere descending from northern to southern poles. The following tables show components retained, using the broken stick criteria, for each biome. Blue (+) and red (−) colors provide a visual representation of major contributors to the PCA gradient. Biome number: 1 = Tropical and Subtropical Moist Broadleaf Forests, 2 = Tropical and Subtropical Dry Broadleaf Forests, 3 = Tropical and Subtropical Coniferous Forests, 4 = Temperate Broadleaf and Mixed Forests, 5 = Temperate Conifer Forests, 6 = Boreal Forests, 7 = Tropical and Subtropical Grasslands, Savannas and Shrublands, 8 = Temperate Grasslands, Savannas and Shrublands, 9 = Flooded Grasslands and Savannas, 10 = Montane Grasslands and Shrublands, 11 = Tundra, 12 = Mediterranean Forests, Woodlands and Scrub, 13 = Deserts and Xeric Shrublands, 14 = Mangroves. Inv = invertebrate, Nect = nectar, Scav = scavenger, Vect = ectothermic vertebrate, Vend = endothermic vertebrate, Vunk = unknown vertebrates, % = percent variation explained by the principal component.

Biomes	Inv	Seed	Fruit	Vend	Vect	Fish	Vunk	Scav	Nect	Plant	%
Nearctic											
11	0.20	−0.25	0.00	−0.01	0.00	0.00	0.00	−0.01	0.00	−0.15	45.60
6	0.20	−0.29	0.05	−0.01	0.00	0.00	0.00	−0.01	0.01	−0.10	48.19
5 west	0.19	−0.30	0.05	−0.01	0.00	0.00	0.00	−0.01	0.01	−0.07	47.49
4 west	0.21	−0.30	−0.02	−0.01	−0.01	−0.01	0.00	−0.01	0.00	−0.10	50.18
8	0.18	−0.30	0.05	−0.01	0.00	0.00	0.00	−0.01	0.01	−0.06	46.45
4 east	0.18	−0.30	0.05	0.00	0.00	0.00	0.00	−0.01	0.02	−0.07	46.94
12	0.19	−0.31	0.03	−0.01	0.00	0.00	0.00	−0.01	0.01	−0.08	48.66
5 east	0.18	−0.29	0.05	−0.01	0.00	−0.01	0.00	−0.01	0.01	−0.04	46.30
13	0.18	−0.30	0.05	−0.01	0.00	0.00	0.00	−0.01	0.01	−0.06	45.84
2	0.16	−0.30	0.07	0.00	0.01	0.00	0.00	−0.01	0.01	−0.03	44.53
7	0.17	−0.29	0.06	−0.01	0.00	0.00	0.00	−0.01	0.02	−0.03	47.04
3	0.18	−0.30	0.05	0.00	0.00	0.00	0.00	0.00	0.01	−0.05	44.41
Neotropic											
3	0.20	−0.14	−0.22	−0.01	0.01	0.00	0.00	0.00	−0.01	−0.04	40.41
13 north	0.21	−0.01	−0.31	0.00	0.00	0.00	0.00	0.00	−0.02	−0.02	43.00
2 north	0.19	−0.01	−0.31	0.00	0.01	0.00	0.00	0.00	−0.01	−0.01	44.55
7 north	0.22	−0.01	−0.32	0.00	0.01	0.00	0.00	0.00	−0.02	−0.01	53.64
14	0.22	−0.04	−0.30	0.00	0.01	0.00	0.00	0.00	−0.02	−0.01	47.11
1	0.24	−0.04	−0.33	0.00	0.01	0.00	0.00	0.00	−0.01	−0.01	61.10
13 east	0.24	−0.22	−0.15	0.00	0.00	0.00	0.00	0.00	−0.01	−0.01	45.22
2 east	0.23	−0.19	−0.19	0.00	0.00	0.00	0.00	0.00	0.00	−0.01	44.36
9	0.24	−0.20	−0.19	0.00	0.00	0.00	0.00	0.00	−0.02	−0.04	50.11
10	0.28	−0.25	−0.14	0.00	0.00	0.00	0.00	0.00	0.01	−0.07	50.19
13 west	0.27	−0.33	−0.02	0.00	0.00	0.00	0.00	0.00	0.01	−0.03	52.59
7 south	0.23	−0.14	−0.24	0.00	0.00	0.00	0.00	0.00	−0.01	−0.03	49.93
2 west	0.25	−0.11	−0.28	0.00	0.01	0.00	0.01	0.00	−0.01	−0.03	50.39
12	0.29	−0.36	0.01	0.00	0.00	0.01	0.00	0.00	0.01	−0.02	69.78
8	0.27	−0.30	−0.05	0.00	0.00	0.00	0.00	0.00	0.00	−0.08	57.22
4	0.28	−0.32	0.01	0.00	0.00	0.01	0.00	0.00	0.00	−0.08	65.32

3.4. Spatial Structure

Eight of the twenty-eight biomes did not yield significant results from the RDA with PCNMs and detrended species by site matrix. The 20 biomes that yielded significant results from the RDA retained 1 to 45 PCNM dimensions ranging from coarse to fine spatial scales (Table 2). The retained PCNM dimensions accounted for 5.90% to 72.74% of the variation in spatial structure (Table 2). When examining the unique contributions of the PCNM (spatial structure) and niche characteristics to passerine distribution, spatial structure had a unique and significant relationship with passerine distribution in 18 biomes (Table 2). Spatial structure accounted for a 3.1% (east temperate conifer forests) to 67.4% (montane grasslands and shrublands) of the variation in the CA components of the passerine distributions.

3.5. Niche Relationships with Distribution

Grinnellian niche characteristics were uniquely and significantly related to distribution in all biomes ($p < 0.05$, Table 5). Grinnellian niche characteristics accounted for between 4.9% (Mediterranean Forest biome) and 93.8% (Tropical Dry Forest biome) of unique variation in CA components of passerine distributions. There was no significant association between latitude ($r_{\text{Spearman}} = -0.06$, $p = 0.747$) or longitude ($r_{\text{Spearman}} < 0.01$, $p = 0.982$) and unique variation accounted for by Grinnellian niche characteristics, thus indicating that there was no latitudinal or longitudinal gradient in the degree to which they related to distribution of species.

Table 5. The relationship between distribution of species and unique Grinnellian and Eltonian niche characteristics and spatial structure were examined using variation partitioning with redundancy analyses within multiple biomes across the western hemisphere. Bolded values indicate a significant amount of variation accounted for in distribution of species. Biome number: 1 = Tropical and Subtropical Moist Broadleaf Forests, 2 = Tropical and Subtropical Dry Broadleaf Forests, 3 = Tropical and Subtropical Coniferous Forests, 4 = Temperate Broadleaf and Mixed Forests, 5 = Temperate Conifer Forests, 6 = Boreal Forests, 7 = Tropical and Subtropical Grasslands, Savannas and Shrublands, 8 = Temperate Grasslands, Savannas and Shrublands, 9 = Flooded Grasslands and Savannas, 10 = Montane Grasslands and Shrublands, 11 = Tundra, 12 = Mediterranean Forests, Woodlands and Scrub, 13 = Deserts and Xeric Shrublands, 14 = Mangroves.

Biomes	Grinnellian			Eltonian			Spatial		
	F	R ² _{adj.}	P	F	R ² _{adj.}	P	F	R ² _{adj.}	P
Nearctic									
11	27.2	38.7	0.002	2.1	3.7	0.006	NA	NA	NA
6	11.9	13.8	0.002	1.6	1.4	0.162	NA	NA	NA
4 west	39.2	50.5	0.002	7.6	15.1	0.002	NA	NA	NA
5 west	8.6	6.4	0.004	2	0.9	0.152	NA	NA	NA
8	41.2	35.4	0.002	1.4	0.4	0.180	5.6	29.9	0.002
4 east	106	69.7	0.002	0.1	<0.1	0.922	13.9	17.5	0.002
12	8.8	4.9	0.002	0.8	<0.1	0.600	1	0	0.478
5 east	39.1	43.7	0.002	1.1	0.1	0.348	5.6	3.1	0.002
13	13.4	16.3	0.002	0.5	1.6	0.176	1.4	1.9	0.126
2	984	93.8	0.002	1	<0.1	0.358	2.9	19.3	0.004
7	11.1	21.3	0.002	0.9	<0.1	0.462	NA	NA	NA
3	70.2	48.2	0.002	1.9	0.8	0.088	NA	NA	NA

Table 5. Cont.

Biomes	Grinnellian			Eltonian			Spatial		
Neotropic									
3	26.2	19.8	0.002	1.3	0.2	0.216	4.6	15.4	0.002
13 north	52.9	42.1	0.002	0.6	<0.1	0.684	23.5	34.3	0.002
2 north	135	60.1	0.002	0.8	<0.1	0.512	63.4	24.5	0.002
7 north	24.9	38.9	0.002	1.2	0.2	0.304	5	27.8	0.002
14	36.4	30	0.002	1.8	0.6	0.124	18.5	67	0.002
1	158	36.7	0.002	1.1	<0.1	0.316	27.4	58.1	0.002
13 east	12.6	15.1	0.002	2.1	1.7	0.052	2.1	13.2	0.002
2 east	29.3	42.1	0.002	2	2.5	0.100	8.6	48.9	0.002
9	13.2	14	0.002	2.5	2	0.048	2.9	11	0.002
10	49.3	45.2	0.002	1.2	0.2	0.330	11.2	67.4	0.002
7 south	61.9	25.8	0.002	0.7	<0.1	0.658	24.3	56.9	0.002
2 west	76.3	59	0.002	3	2.5	0.032	13	51.6	0.002
13 west	21.3	18.3	0.002	0.9	<0.1	0.434	3.5	9.6	0.006
12	11.7	28.7	0.002	0.5	0	0.634	NA	NA	NA
8	31.4	16.5	0.002	3.6	3.2	0.002	4.7	13.8	0.002
4	33.2	49.8	0.002	0.7	<0.1	0.496	NA	NA	NA

Eltonian niche characteristics were uniquely and significantly related to distribution for only 5 out of 27 biomes (Table 5). For biomes that exhibited a significant relationship, Eltonian niche characteristics accounted for between 2% (flooded grasslands and savannas) and 15.1% (western temperate broadleaf and mixed forests) of the variation in the CA components of the passerine distributions. There was no significant relationship between latitude ($r_{\text{Spearman}} = 0.22$, $p = 0.262$) or longitude ($r_{\text{Spearman}} = 0.05$, $p = 0.815$) and unique variation from the RDA between Eltonian niche characteristics and the distribution of species.

3.6. Phylogenetic Structure with Niche Characteristics

Principal coordinates analysis used to examine the phylogenetic structure for each biome yielded between 3 and 18 axes based on the broken stick criterion. Retained axes accounted for between 51.79% and 69.92% of the variation in avian phylogenetic distances. Phylogenetic signals in Eltonian niche characteristics were present (Table 6) across all biomes, with phylogenetic structure accounting for 7.5% (12) to 56.1% (4) of the variation among species. There was no significant correlation between variation accounted for by phylogenetic structure in species Eltonian niche characteristics across latitudes ($r_{\text{Spearman}} = -0.14$, $p = 0.475$) or longitudes ($r_{\text{Spearman}} = 0.26$, $p = 0.186$).

Grinnellian niche characteristics and phylogenetic relatedness were significantly related in 10 Neotropical biomes and 3 Nearctic biomes (Table 6). Phylogenetic structure accounted for 2.1% (Tropical and Subtropical Dry Broadleaf Forests) to 15.7% (Mediterranean Forests and Woodlands and Scrub) of significant variation across biomes (Table 6). There was no significant correlation between the phylogenetic structure of the Grinnellian niche characteristics across latitudes ($r_{\text{Spearman}} = -0.326$, $p = 0.091$) or longitudes ($r_{\text{Spearman}} = 0.07$, $p = 0.706$).

Table 6. Redundancy analyses conducted on phylogenetic structure (created with principal coordinate analyses) and passerine Grinnellian and Eltonian niche characteristics in multiple biomes across the latitudinal gradient. Bolded values indicate significance. Axes are the number of phylogenetic components retained following the broken stick criterion. Biome number: 1 = Tropical and Subtropical Moist Broadleaf Forests, 2 = Tropical and Subtropical Dry Broadleaf Forests, 3 = Tropical and Subtropical Coniferous Forests, 4 = Temperate Broadleaf and Mixed Forests, 5 = Temperate Conifer Forests, 6 = Boreal Forests, 7 = Tropical and Subtropical Grasslands, Savannas and Shrublands, 8 = Temperate Grasslands, Savannas and Shrublands, 9 = Flooded Grasslands and Savannas, 10 = Montane Grasslands and Shrublands, 11 = Tundra, 12 = Mediterranean Forests, Woodlands and Scrub, 13 = Deserts and Xeric Shrublands, 14 = Mangroves. % = percent variation explained by the principal coordinate analysis.

Biomes	Grinnellian			Eltonian			Axes	%
	F	R ² _{adj.}	P	F	R ² _{adj.}	P		
Nearctic								
11	1	0	0.472	5.4	20.9	0.002	4	53.06
6	0.9	0	0.534	8.3	22.1	0.002	4	51.79
4 west	1.7	4.5	0.114	5.2	22.3	0.002	4	53.18
5 west	1.8	4.7	0.026	9.5	34.6	0.002	11	65.79
8	1.3	1.5	0.134	9.9	32.4	0.002	10	63.5
4 east	0	0.6	0.954	10.8	35.9	0.002	8	60.01
12	1.6	3	0.176	26.2	7.5	0.002	7	57.13
5 east	0.5	0	0.904	6.9	21.6	0.002	5	56.89
13	2.6	8.2	0.002	11.2	36.4	0.002	12	67.33
2	1.7	3.1	0.174	3.6	10.8	0.004	3	52.54
7	1.9	4.5	0.012	7.7	26.2	0.002	6	58.82
3	1.5	2.4	0.052	10.7	32.4	0.002	9	61.84
Neotropic								
3	3.8	11.8	0.002	10.7	32	0.002	13	68.04
13 north	2.6	6.7	0.002	8.9	26.5	0.002	9	63.83
2 north	1.7	2.1	0.006	14.5	30.9	0.002	11	66.83
7 north	1.3	1.4	0.142	10.1	29.2	0.002	7	63.84
14	2	3.9	0.004	13.7	34.1	0.002	10	67.49
1	6.2	11	0.002	33	43.3	0.002	18	69.92
13 east	1.7	2.5	0.076	12	27.7	0.002	5	60.64
2 east	1.6	2.8	0.148	10.6	32	0.002	4	60.99
9	1.7	2.7	0.058	11.2	28.6	0.002	6	65.31
10	2.3	5	0.004	10.4	28.4	0.002	8	66.06
7 south	4.2	7.8	0.002	18.9	31.9	0.002	9	65.14
2 west	1.6	2.5	0.06	10.8	29.5	0.002	7	64.08
13 west	3.3	7.5	0.02	12.2	28.3	0.002	3	59.75
12	3.1	15.7	0.01	64.9	22.3	0.002	4	61.74
8	2.1	3.7	0.046	17.4	35.3	0.002	5	62.36
4	1.2	1.5	0.294	15.8	56.1	0.002	5	66.32

4. Discussion

Even after accounting for spatial structure, the Grinnellian niche characteristics had a stronger relationship with the passerine distribution compared to the Eltonian niche characteristics for all biomes. Moreover, different Eltonian and Grinnellian niche characteristics had differing importance across biomes. The phylogenetic signal was present in the Grinnellian niche characteristics for 46% of the biomes. In contrast, Eltonian niche conservatism existed across all biomes. There was stronger phylogenetic signal with dietary characteristics than abiotic conditions, and there was no apparent latitudinal pattern in the phylogenetic signal or the degree to which niche characteristics relate to distributions of species.

Only a few studies have used both the Eltonian and Grinnellian niches to examine distribution. Studies that have used both concepts have discovered that Eltonian niche

characteristics are significantly related to distribution, but the relationships are weak compared to Grinnellian niche characteristics (passerines [28], felids [87], bats [68]). Olalla-Tárraga [28], Sánchez-Barradas and Villalobos [87], and Stevens [68] demonstrated that distributions of species were mediated more by abiotic conditions than by dietary components. Similarly, this study demonstrated that the relationships between distribution and Eltonian niche characteristics were weak or not apparent.

4.1. Eltonian Niche Characteristics

Eltonian niche characteristics have driven a number of hypotheses regarding latitudinal diversity gradients [7,20]. Although the Eltonian niche characterizes resource–consumer dynamics and biotic interactions, spatial and temporal heterogeneity, as well as complexity, may make it challenging to measure biotic interactions, specifically competition [88]. Moreover, studies investigating negative biotic interactions and their influence on diversity at the equator have not found evidence supporting the competition hypothesis [89,90]. Some studies have demonstrated predation as a stronger driving force in the tropics than in temperate regions. For example, tropical birds had higher rates of nest predation than temperate birds [91,92]. However, additional research is necessary to thoroughly examine the correlation between predation rates and latitude [93]. The niche breadth hypothesis predicts that niche breadth is narrower at lower latitudes, but this hypothesis has little empirical support [94]. Instead, increasing dietary overlap is often positively related to species diversity [68]. The absence of a relationship between passerine distribution and Eltonian niche characteristics may be due to many species being dietary generalists, to the spatial scale of this study may be too coarse, or because of a lack of more precise dietary information.

We did find that the importance of frugivory compared to granivory shifted from the equator toward the poles. Running a Spearman’s correlation on absolute latitude and PCA loadings of Eltonian niches yielded a significant result for frugivory ($r_{\text{Spearman}} = 0.73$, p -value < 0.001) and granivory ($r_{\text{Spearman}} = -0.68$, p -value < 0.001). Birds in South America exhibit a greater propensity towards frugivory than their North American counterparts [95,96], thus potentially due to the increased abundance of fruit towards the equator [97]. Granivory might prevail more in temperate regions due to heightened seed dormancy, thereby increasing resource availability in areas with seasonal environments, such as deserts [98–101]. Moreover, seeds contain high amounts of energy [102]. Given the high energy costs associated with the reproductive period [103], seeds could serve as a sustainable and energetically efficient food source in temperate regions. Therefore, the variation in resource availability and energy needs during reproduction along latitudinal gradients may determine the significance of granivory and frugivory in temperate and tropical regions, respectively.

The weak to absent relationship between Eltonian niche characteristics and passerine distribution across biomes and latitudes may be rooted in data accessibility (Eltonian shortfalls [88]). Climatic variables are widely used in species distribution models because they are readily accessible [1]. Information on Eltonian niche characteristics is less common because this information is temporally and spatially heterogeneous and difficult to obtain [88]. While this study would benefit from including more information on Eltonian niche characteristics, we doubt there would be a stronger relationship between Eltonian niche characteristics than Grinnellian niche characteristics regarding passerine distributions. The Grinnellian niche explained a significant portion of the variation, up to 93.8%, in the passerine distribution, whereas the Eltonian niche contributed to no more than 15.1% of the variation in species distribution. It is difficult to conceive that additional data on Eltonian niche characteristics would match or surpass the importance of Grinnellian niche characteristics.

4.2. Grinnellian Niche Characteristics

The strong relationship between the Grinnellian niche characteristics and passerine distribution may be due to dispersal capabilities, as higher mobility may allow species to have access to more environmentally suitable locations [104]. More vagile species may have stronger responses to climatic changes [105], whereas biotic interactions and resource availability may be more influential in the distribution of less mobile organisms (barnacles [106] and microinvertebrates [107]). Dispersal capability may influence the ability of a species to colonize certain patches. For example, competitor–colonizer tradeoffs can facilitate spatial coexistence among competitive species [105]. Under such a scenario, a superior competitor tends to be a poor disperser, whereas the inferior competitors tend to be good dispersers [105]. The heightened dispersal capability of passerines might explain why they exhibit a more pronounced relationship to environmental conditions compared to dietary needs.

Elevation was an important component for passerine distributions across most biomes, whereas the importance of other Grinnellian niche characteristics varied across biomes (Table 3). While tropical regions are considered climatically stable environments compared to temperate areas, elevation gradients provide substantial habitat heterogeneity that may influence geographic distributions. In the tropics, there is an inverse relationship between elevation, temperature, and vegetation (abiotic conditions) that has a greater impact on community composition than resource availability (biotic filters [108]). Elevational gradients may help explain why the distributions of passerines were significantly related to Grinnellian niche characteristics in tropical regions.

The different importance of human impact, AET, temperature, and precipitation on the passerine distribution may be attributed to habitat heterogeneity, complexity, or quality that was unaccounted for. Biomes, classified by vegetation and climatic conditions, are divided further into ecoregions encompassing distinct communities and species distributions [36]. Approximately 275 distinct ecoregions were within the 27 biomes used in this study. Increased habitat heterogeneity is linked to increased species richness, thus peaking between transition zones of ecoregions and biomes [109,110]. Transitions across ecoregions (e.g., short grasses to tall grasses) or biomes (e.g., grasslands to forest) increase habitat heterogeneity and horizontal and vertical complexity, which are important axes of heterogeneity for birds. Habitat complexity increases even further at finer spatial scales, with resource availability and abundance influencing species distribution [111]. Habitat quality can further influence distribution patterns. Cities are often associated with decreased primary productivity and biodiversity compared to surrounding more natural environments [67]. However, increased net primary productivity and water within cities can increase avian abundance in arid ecosystems [112]. Therefore, variations in the complexity and heterogeneity of AET and climatic conditions, along with the landscape context of urban areas affecting habitat quality, could result in differences in the importance of niche characteristics.

4.3. Niche Conservatism

We expected a latitudinal gradient in phylogenetic niche conservatism to reflect passerines diversifying their niche to colonize temperate regions. However, we did not find a relationship between the phylogenetic signal and latitude, but niche conservatism was strongest in the biomes in South America. The absence of a discernible pattern may be attributed to the evolutionary history of birds. Birds colonized the Neotropics when South America was an island approximately 50 million years ago [32]. While birds dispersed to the Nearctic during the separation, the great exchange only occurred once the Isthmus of Panama was formed 3.5 million years ago [113]. Grinnellian and Eltonian niche conservatism was stronger in the Neotropics than in the Nearctic realm, thus potentially due to species having more evolutionary time in the Neotropics than in the Nearctic realm. Examining niche conservatism from the equator to both poles potentially dilutes the latitudinal

gradient. Niche conservatism is likely more evident when transitioning from tropical to Nearctic regions.

After colonizing and diversifying in South America [114], expanding to North America would have been difficult due to strong phylogenetic niche conservatism. Gómez et al. [115] found that migrant Paridae (family within Passerines) had wider, overlapping climatic niches than nonmigratory birds. Nonmigratory birds had greater variation in their climatic niche and were more specialized than migratory species [115]. While we found a relationship between phylogenetic structure and Grinnellian niche characteristics, it was weak, thus decreasing the effects of niche conservatism as a filter. Therefore, higher mobility may allow passerines to colonize locations that are more suitable for their Grinnellian niche, and weak niche conservatism may not limit migration to the Nearctic realm.

There have been very few studies that have examined the evidence of Eltonian niche conservatism in birds, with some studies demonstrating dietary niche conservatism (e.g., [116,117]), and another study that found a lack of support in birds (e.g., [118]). Brändle et al. [117] found that migratory birds had narrower dietary niches (highly correlated with phylogenetic signal) than nonmigratory birds. The significance of phylogenetic signal observed in Eltonian niche characteristics, as evidenced in this study, suggests that it may not act as a barrier for passerines colonizing locations across latitudes during migration. However, as conditions become less favorable (e.g., winter), the strength of the filter may increase, thus forcing birds to return to their nonbreeding grounds.

5. Conclusions

It is important to mention that we only examined a portion of the passerine Grinnellian and Eltonian niches. Besides the addition of other Eltonian niche characteristics, other components of the Grinnellian niche may provide additional insight into the responses of species to environmental gradients, such as responses to fragmentation, agriculture, shifting climates, and habitat complexity. However, gathering information that covers such a broad spatial scale may be difficult to achieve. Additionally, the consideration of additional resources such as nesting locations, more in-depth dietary information, or greater geographic resolution of food resources may be necessary to better understand Eltonian niches. Moreover, we relied on digital information on passerine distribution, which presents limitations and biases that we discussed in the methods but also limits information in more remote areas away from civilizations. Additionally, there was less available bird information in the Neotropics than in the Nearctic region, thus probably due to the barriers faced by Neotropical ornithologists that need to be recognized [119]. Despite all this, we determined that passerine distribution has a greater response to environmental conditions than to dietary resources. Tropical regions were found to be variable in abiotic factors (Table 1), which could be a major filter influencing the distribution of species. Grinnellian niche conservatism was present in a few biomes, which may prevent species from colonizing novel areas. With climate and anthropogenic changes increasing, it is necessary to examine if species can tolerate these changes or if they may face extinction due to retaining ancestral traits that no longer benefit them in these new and ever-changing conditions.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d16060352/s1>. Table S1: Principal component analyses conducted on Grinnellian niche characteristics of birds from biomes the western hemisphere descending from northern to southern poles. Principal components were retained using the broken stick criteria. Principal coordinates analysis loadings for each variable are presented with blue to red representing the major contributors to the gradient. The following tables show components retained for each biome; Table S2: Principal component analyses conducted on Eltonian niche characteristics of birds from biomes the western hemisphere descending from northern to southern poles. Principal components were retained using the broken stick criteria. Principal component analysis loadings for each variable are presented with blue to red representing the major contributors to the gradient with points being outside the 50th percentile. The following tables show components retained for each biome; Figure S1: Correspondence analyses were conducted on distribution of species throughout the major biomes in the western hemisphere. Biomes (and biome numbers) are listed from northern pole to southern pole. Dimensions were retained by using the elbow technique. Only one dimension was retained for the tropical dry forest (2). Gradients are described for each dimension.

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