Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography | A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

The Productivity Gradient Explains Global Bird Specialisation Better Than Climate Stability

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Received: 5 February 2025 | **Revised:** 26 July 2025 | **Accepted:** 30 July 2025

Handling Editor: Catherine Sheard

Funding: R.M. was supported by a JAE Intro-CSIC internship (JAEINT_23_02188). C.M.N. was supported by the 'Juan de la Cierva' programme (ref. FJC2021-046829-I) and a Junta de Andalucia and FSE+ grant (ref. DGP_POST_2024_00228). V.G.N. received funding from Agencia Estatal de Investigación (grant ref. CNS2023-144066).

Keywords: bird assemblages | climate specialisation | climate stability hypothesis | diet specialisation | environmental filtering | evolutionary age | global patterns | niche breadth | species richness

ABSTRACT

Aim: Historical and contemporary environmental factors are hypothesised to influence the degree of ecological specialisation of species. Long-term climate stability might facilitate specialisation by promoting stable environments and diversification (climate stability hypothesis). In contrast, current stress–productivity gradients could also moderate specialisation through: (i) environmental filtering in stressful (e.g., arid) environments or (ii) accumulation of specialised species in highly productive regions.

Location: Global.

Time Period: Pliocene-present.

Major Taxa Studied: Birds.

Methods: We tested whether different specialisation facets (climate, diet and habitat) in bird assemblages are better explained by long-term climate stability or current stress-productivity gradients while accounting for latitude, longitude, biogeographic realm, taxonomic species richness and the evolutionary age of the assemblages at a global scale.

Results: Long-term climatic stability was a weak predictor of bird specialisation after accounting for latitude. In contrast, aridity showed a consistent negative association with climate, diet, and habitat specialisation, even after controlling for latitude and species richness. Species richness was strongly positively associated with diet specialisation, suggesting the influence of niche filling processes. In addition, specialisation was more pronounced in high-productivity environments, indicating that greater niche availability fosters specialisation. Notably, the effects of aridity and assemblage mean evolutionary age on specialisation differed between hemispheres. While negative associations dominated in Southern realms, the Palearctic and Nearctic realms in the Northern Hemisphere showed more positive trends. This hemispheric contrast underscores the context-dependency of environmental effects on specialisation and points to biogeographic history as a potential modulator of these patterns.

Conclusions: Globally, stress-productivity gradients better explain patterns of avian specialisation than long-term climate stability. Overall, our results did not support the climate stability hypothesis and challenged the idea that abiotically stressful conditions promote specialisation. The present study suggests that ecological processes, especially niche filling in productive regions with accumulated species, play a key role in driving and maintaining specialisation in birds.

1 | Introduction

Understanding the ecological and evolutionary drivers of species specialisation is crucial for elucidating the mechanisms that give rise to the diverse ecological strategies observed in biological communities worldwide. Specialisation, defined as the narrowness of the sets of environments or resources a species can exploit (Devictor et al. 2010), constitutes a core concept to understand biological adaptations (Sexton et al. 2017), predict biological invasions (Daly et al. 2023), assess species extinction risk (Morelli et al. 2021; Martínez-Núñez et al. 2023a) and explain the processes underlying global biodiversity patterns (Willig et al. 2003). In this sense, three hypotheses aimed at explaining broad species specialisation patterns, focusing on species richness, climate stability and environmental stress, have been postulated but have never been tested in combination.

The richness-specialisation hypothesis posits that specialisation arises as a strategy to avoid competition and, therefore, allow coexistence in species-rich communities (Belmaker et al. 2012; Pellissier et al. 2018; Pigot et al. 2016). Hence, specialisation may be fostered in species-rich communities as a means to avoid interspecific competition (Granot and Belmaker 2020). In the tropics—regions known for their exceptionally high species richness and rapid diversification rates (Jetz et al. 2012; Antonelli et al. 2018)—these dynamics may lead to the formation of more specialised assemblages. This pattern aligns with the latitudinal gradient often associated with specialisation, in a way that the degree of niche variation increases toward lower latitudes since individual niches become increasingly narrower and more disparate (Araújo and Costa-Pereira 2013; Vázquez and Stevens 2004). Therefore, if specialisation is primarily an adaptive response to competition, we would expect to find greater levels of specialisation in more species-rich assemblages. At the same time, ecological specialisation is often viewed as an evolutionary 'dead-end' that limits further evolution (Futuyma and Moreno 1988). Although transitions in the opposite direction are also plausible (i.e., generalists evolving from specialists) (Day et al. 2016), one would expect a higher predominance of generalists in the basal lineages (Nosil and Mooers 2005). In addition, the release of specialists from competition could, in certain ecological contexts, trigger niche filling diversification, potentially leading to increased speciation rates in specialist clades under favourable conditions (Schluter 2000). Consequently, we also expect a higher level of ecological specialisation in evolutionarily younger assemblages. In this way, examining the interplay between species richness, assemblage age and specialisation can offer insights into the ecological and evolutionary processes driving niche differentiation within biological communities (Colles et al. 2009; Vamosi et al. 2014).

Both past (i.e., long-term climatic stability) and current climates may influence specialisation through two main mechanisms. First, as proposed by MacArthur (1955), regions with greater long-term climate stability may support more specialised taxa. The absence of major climatic disruptions can promote population stability over generations, enabling species to diversify and specialise in particular environments and ecological functions (Rodrigues-Filho et al. 2018). However, a recent meta-analysis found limited support for this climate-stability hypothesis, suggesting instead that high species richness promotes community-level specialisation by shaping the assembly of species with narrower niches (Granot and Belmaker 2020). This implies that patterns of specialisation would be more driven by ecological processes, such as competition and resource partitioning within diverse communities, rather than by evolutionary changes, such as speciation (Granot and Belmaker 2020). Second, current climatic conditions can also drive specialisation by favouring niche specialists that perform better under certain environmental conditions. For example, in benign climates that sustain high primary productivity, species may experience an evolutionary trade-off between exploiting a broad range of resources and optimising the use of specific resources (MacArthur 1972; Richards et al. 2006). This jack-of-all-trades concept suggests that restricted ecological niche breadth arises from this generalist-specialist trade-off, which is likely reinforced in competitive environments where specialisation confers an advantage. In addition, environmental filtering can shape communities in climatically stressful conditions, such as xeric environments or regions with extreme temperatures, where only species with certain traits can thrive (e.g., Swenson et al. 2012; Rivas-Salvador et al. 2019). In such environments, environmental filtering may favour highly specialised species adapted to the specific stressor or could also promote generalist species able to cope with a wide range of abiotic conditions (Devictor et al. 2008; Wiens et al. 2013). Although these factors may help explain the emergence and persistence of specialisation, there is a lack of studies exploring how both past and contemporary climates have shaped global patterns of climate, diet and habitat specialisation in animals (Wiens et al. 2013).

There are different ecological dimensions or axes along which species can specialise, such as habitat, diet and climate, each potentially responding differently to (changes in) environmental conditions (Futuyma and Moreno 1988; Clavero and Brotons 2010; Morelli et al. 2019; Di Cecco and Hurlbert 2022). Hence, a given species might simultaneously be a generalist on one axis (e.g., omnivorous in terms of diet) and a specialist on another (e.g., habitat requirements). For instance, climatic specialisation could be influenced by climatic stability, with more stable regions fostering climatically specialised communities adapted to consistent and predictable conditions. In contrast, diet specialisation may be primarily driven by resource availability or biotic interactions such as interspecific competition (Barnagaud et al. 2019). Considering these distinct facets of specialisation clarifies the interaction between environmental and biotic factors in shaping specialisation across different ecological contexts. Yet, to our knowledge, few studies have considered these three axes of specialisation together.

In this study, we investigated the relative contributions of species richness, evolutionary age, long-term climate stability and current climatic conditions (i.e., using aridity as a proxy of environmental harshness and the stress-productivity gradient) in shaping the degree of climatic, dietary and habitat specialisation in bird assemblages at a global scale. We use birds as a study system due to their global distribution, ecological diversity and well-documented traits, allowing robust analyses. Specifically, we estimated specialisation indices for a total of 9709 bird species. Using these values, we calculated average specialisation values for species assemblages across 15,729 grid cells spanning six major biogeographic realms.

We analysed how assemblage specialisation indices relate to long-term climate stability and present climatic conditions, accounting for species richness and assemblage evolutionary age. We expect that: (i) Overall specialisation will be greater in species-rich assemblages and those with younger evolutionary histories. We also anticipate higher specialisation in arid and climatically stable environments, even after accounting for species richness; (ii) Climatic specialisation will be particularly high in regions that have experienced long-term climatic stability; (iii) Diet specialisation will increase with species richness and younger assemblage age, reflecting niche filling processes that reduce competition and support coexistence; (iv) Habitat specialisation will be greater in drier environments, consistent with environmental filtering effects.

2 | Methods

2.1 | Bird Spatial Data

We acquired spatially explicit bird occurrence data from the AVONET database (Tobias et al. 2022), which is based on BirdLife International's current species distribution ranges (https://datazone.birdlife.org). In AVONET, species distributions were extracted and mapped onto a global equal-area grid using Behrmann projection at a resolution of one degree (~110 km side grid cells). Although this resolution is relatively coarse and does not capture fine-scale community-level responses, it is widely used in global analyses to identify broad biogeographic patterns (Barnagaud et al. 2017; Belmaker et al. 2012; Martínez-Núñez et al. 2023b). Moreover, due to the inherent imprecision in global bird range maps, increasing grid resolution would not significantly improve accuracy but would raise computational costs. AVONET provides species occurrences per grid cell derived only from distribution ranges designated as native breeding, reintroduced breeding, or resident breeding sites, ensuring biologically meaningful presence data. In total, 18,709 terrestrial grid cells covering the entire terrestrial part of the Earth were initially considered. We excluded grid cells that contained fewer than three bird species and those with less than 10% of land (primarily open ocean). Ultimately, 15,731 grid cells were used for analyses, belonging to the six main biogeographic realms: Nearctic (2616 grid cells), Neotropic (2255), Palearctic (6123), Afrotropic (2462), Australasian (1199) and Indomalayan (1076).

2.2 | Specialisation Indices

We calculated three different dimensions of specialisation for each of the 9709 bird species considered. We include marine species given their presence in coastal and terrestrial areas.

First, the *climatic specialisation index* was computed as the arithmetic mean between two sub-indices regarding seasonality in temperature and precipitation. The former subindex represented the difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month (i.e., Bio5 and Bio6 variables in WorldClim), and the latter represented the difference between precipitation of the wettest month and precipitation of the driest month (i.e., Bio13 and Bio14), both across the breeding distribution range of each species (see Figures S1.1 and S1.2 for differences between two sub-indices). In addition, we estimated the range of maximum and minimum temperatures and precipitation only considering the months when migratory species would occupy their breeding area in the Northern Hemisphere (May–August), where these species can be a significant proportion of bird assemblages (Somveille et al. 2015). However, for simplicity, and given that the results were virtually the same, we show in the main text the results of the first approach (see Figures S1.3 and S1.4 for a sensitivity analysis concerning migratory species). Climatic data were collected from WorldClim version 2.1 (www.worldclim.org) and extracted to the same resolution as our bird assemblage data using 'zonal statistics' with 'terra' (Hijmans 2023) and 'sf' packages (Pebesma 2018). To allow comparisons with diet and habitat specialisation, we normalised this index, constraining it between 0 (minimum specialisation) and 1 (maximum specialisation).

The *diet specialisation index* was estimated based on the percentages of the 10 major food items (invertebrates, endotherm vertebrates, ectotherm vertebrates, vertebrate fishes, unknown vertebrates, carrion, fruits, nectar, seeds and plants) reported in Wilman et al. (2014). Following Morelli et al. (2019), we estimated the degree of diet specialisation of each species using the Gini index of inequality (Cowell 2011). The Gini coefficient measures statistical dispersion and oscillates between 0 and 1, indicating the lowest and highest specialisation scores, respectively.

The *habitat specialisation index* for each species was estimated using a similar approach to that employed for diet specialisation, as followed by Belmaker et al. (2012). We retrieved the breeding and resident habitats each species can occupy from the IUCN API v.3 (IUCN 2023) with the 'rredlist' package (Gearty and Chamberlain 2022), and then computed the Gini index. We considered 59 terrestrial and marine habitat categories according to the IUCN habitat scheme (see Appendix S2 for more details). Although this methodology has been adopted in previous studies, the IUCN habitat classification criteria are not specifically designed for birds. Therefore, we ran a sensitivity analysis to assess the potential bias introduced in the habitat specialisation index due to habitat classification by calculating the compositional dissimilarity (beta diversity) of bird assemblages among habitat categories. Habitat categories with very similar species compositions were merged into a single category. After recalculating habitat specialisation based on different scenarios, no differences were found in the results (see Appendix S2).

Lastly, the community mean for the three indices was calculated for each species assemblage (i.e., for every grid cell) to obtain an index of assemblage specialisation.

2.3 | Explanatory Variables

We used two main environmental predictors, the *Aridity Index* (AI) computed by Zomer et al. (2022), which represents the ratio of precipitation to potential evapotranspiration, and the *Climate Stability Index* (CSI). The aridity index (i.e., the ratio of precipitation to potential evapotranspiration) provides a reliable measure of moisture availability for plant growth, which influences bird diversity (Mittelbach et al. 2001). High AI values

indicate environments characterised by water limitations and unpredictability in precipitation, which result in low biomass and large spatio-temporal variation in food resources (Maestre et al. 2016). These features, generally in combination with high temperatures and other abiotic attributes associated with aridity, constitute significant stressors for local taxa, shaping community composition.

The CSI provides information about the stability of climatic variables at high resolution (ca. 5 km) (Herrando-Moraira et al. 2022). This index was estimated by calculating the median of the standard deviation of a set of bioclimatic variables for 12 periods from the Pliocene (3.3 Ma) to the present, representing warming and cold cycles. For the sake of clarity and a better understanding of results, we used the inverse values of these two indices so that the higher the value of the index, the higher the aridity and climate stability.

In addition, we characterised species assemblages in terms of species richness and evolutionary age. Species richness is considered an important correlate of ecological specialisation (e.g., Belmaker et al. 2012) and thus must not only be assessed as a predictor but also taken into account, including it as a covariate when attempting to ascertain the relative contribution of the other predictors. In addition, using the most comprehensive bird phylogeny to date (Jetz et al. 2012), we obtained a consensus tree from 1000 trees using the *maxCladeCred* function from the R package 'phangorn' (Schliep 2011). Then, the evolutionary age was calculated for every species as the distance between each species' nodes and the maximum branch length of the tree, using 'caper' and 'ape' packages, respectively (Orme et al. 2023; Paradis and Schliep 2019). In a final step, we obtained the average evolutionary age for each bird assemblage by computing community means.

2.4 | Statistical Analyses

Before modelling, we assessed potential interdependence among explanatory variables (i.e., species richness, assemblage evolutionary age, climate stability, aridity index, latitude and longitude) by calculating pairwise Pearson correlation coefficients (Figure S1.5). Since CSI and latitude were highly correlated ($\rho = 0.69$), and latitude was necessary to account for spatial autocorrelation, we fitted increasingly complex models. In this way, it is possible to identify possible multicollinearity issues and assess the relative importance of each variable, without losing interpretability as with a PCA approach. All models were fitted using beta regression with a logit link function, implemented via the betareg package in R and estimated using maximum likelihood (Cribari-Neto and Zeileis 2010). All explanatory variables were previously normalised (between 0 and 1). Our replication unit was each grid cell ($n = 15{,}729$).

We fitted four different types of models. First, to examine the predictive capacity of each explanatory variable (i.e., aridity, climate stability, species richness and assemblage mean evolutionary age), we fitted simple beta regression models (i.e., specialisation index ~ explanatory variable). This first step allowed us to estimate the relative importance (i.e., raw predictive power) and unique contribution of each explanatory variable, which can be obscured when correlated variables are included together in the same model (see Martínez-Núñez et al. 2023b for a similar approach). Secondly, to get unbiased estimates for each explanatory variable, we fitted models that incorporated the midpoint coordinates (i.e., longitude and latitude) of grid cells as covariates to account for broad-scale spatial autocorrelation. As some explanatory variables were correlated with latitude (Figure S1.5), we checked for multicollinearity using the variance inflation factor (criteria: VIF < 5). Thirdly, we fitted two models, one for aridity and another for the CSI, in which we included coordinates and species richness as covariates to account for the effects of spatial autocorrelation and species richness, respectively. Subsequently, we examined the marginal mean effects of the predictors using the 'emmeans' R package (Lenth 2023). Lastly, given that biogeographic realms explained a great proportion of the variation in specialisation, we also fitted separate beta regression models for each biogeographic realm. We did not include the biogeographic realm as an interaction factor because models with this interaction suffered from high variance inflation (realm × variable = VIF > 10).

We used AIC and pseudo-R^2 (i.e., the proportion of variance explained by the model, akin to the R^2 in linear regression) to compare model performances, as well as estimates, standard errors and confidence intervals to determine the directionality and strength of the associations. We inspected all the model residuals to ensure they were independent of predictors and normally distributed. Spatial autocorrelation was relatively weak and localised, with no important effects on the results (Figure S1.6). In addition to the beta regression models, we fitted generalised additive models (GAMs, $k = 6$) to check for the presence of nonlinear relationships between specialisation and explanatory variables. The adjustment of $k = 6$ provides a balanced compromise between nonlinearity and overfitting.

All analyses were conducted in the R v.4.4.2 environment (R Core Team, 2024).

3 | Results

The level of specialisation of bird assemblages depended strongly on the biogeographic realm (Figure 1), being the variable that best explained the three studied facets of specialisation (Table 1). Assemblages from the Indomalayan, Nearctic and Palearctic bioregions (i.e., the Northern Hemisphere) showed lower values of climatic specialisation (Figure 2). Diet specialisation was remarkably high in the Neotropics (estimate = 0.89), while habitat specialisation showed a strong difference between the American realms (Nearctic and Neotropic) and the remaining realms (i.e., Afrotropic, Australasian, Indomalayan and Palearctic realms), being higher in the Americas (Figure 2).

3.1 | Climate Specialisation

Climate specialisation was strongly linked to latitude ($R^2 = 0.39$; Table 1), with higher specialisation in assemblages closer to the equator (Figure 1). Other relevant predictors for climate specialisation included taxonomic richness ($R^2 = 0.28$), CSI and evolutionary age (Table 1), with specialisation being higher in older

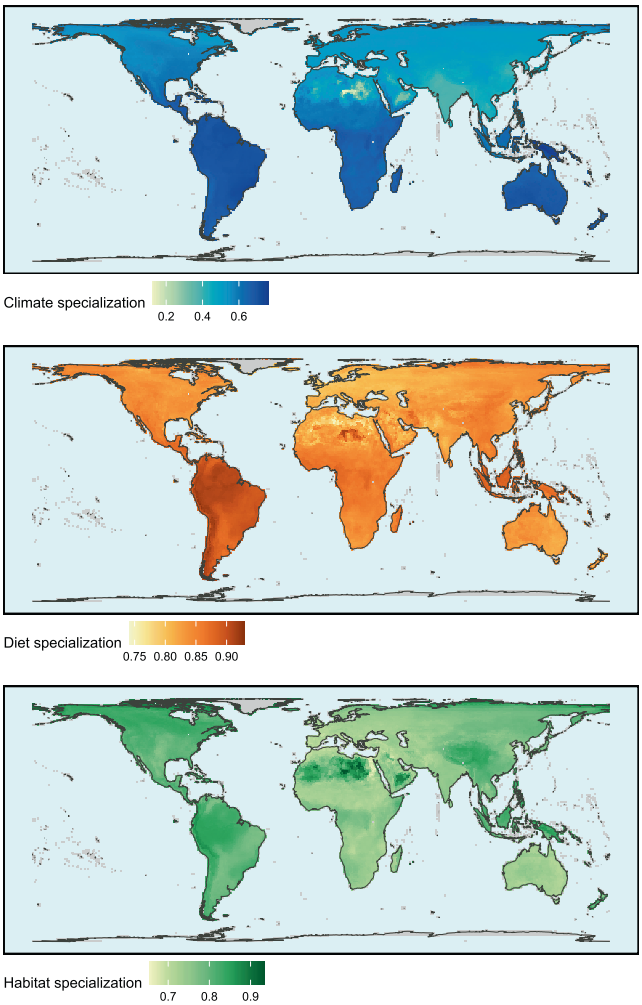

FIGURE 1 | Worldwide distribution of bird specialisation. Observed distribution of the three bird specialisation indices (climate, diet and habitat). Values represent mean assemblage specialisation scores calculated across 15,731 terrestrial grid cells at a spatial resolution of 1°. Grey cells indicate areas excluded from the analysis (i.e., cells with fewer than three species or less than 10% of land). Specialisation indices were normalised across all 9,709 bird species, ranging from 0 (generalist) to 1 (specialist).

and richer assemblages and in assemblages of regions with more stable climates (estimate = 0.84).

We obtained a similar trend after controlling for spatial autocorrelation; species richness and evolutionary age remained as significant predictors, both showing a positive relationship with climate specialisation (Figure 3). Aridity showed a negative association, while the contribution of CSI was significant (Figure 4) but non-substantial in these models (Figure 3).

3.2 | Diet Specialisation

Diet specialisation was strongly associated with species richness, which emerged as the primary predictor in single-predictor models ($R^2 = 0.40$; Table 1). Species richness exhibited a consistent positive effect across all analyses, even when spatial autocorrelation was considered (estimate = 0.73; $\Delta R^2 = 0.15$). Latitude (estimate = −0.53; $R^2 = 0.26$), aridity (estimate = −1.05; $R^2 = 0.16$) and evolutionary age (estimate = −2.41; $R^2 = 0.19$) were also significant predictors, all showing negative effects on diet specialisation, whereas CSI exhibited a low predictive power (estimate = 0.46; $R^2 = 0.09$).

After accounting for spatial autocorrelation, the negative relationship between aridity and diet specialisation remained significant (estimate = −0.92; $\Delta R^2 = 0.12$); whereas CSI and evolutionary age explained little variation in diet specialisation (Figures 3 and 4). Notably, realm-specific models revealed that for the Nearctic realm, aridity had a weak but positive effect on diet specialisation, while in the remaining realms, such a relationship was predominantly negative (Figures S1.7 and S1.8).

3.3 | Habitat Specialisation

Habitat specialisation exhibited distinct patterns compared to climate and diet specialisation. Species richness did not explain a significant proportion of the variance; while CSI and aridity were more influential, both having negative effects (Table 1). Longitude emerged as a better predictor than latitude (Table 1).

Models accounting for spatial autocorrelation supported these findings; aridity and CSI showed significant negative effects on habitat specialisation (Figure 4, Table S1). Evolutionary age again exhibited a strong positive relationship, indicating that older lineages are more specialised, while species richness had a small contribution to the total variance (Figure 3, Table S1). At the realm level, the effects of aridity differed between realms from the Northern and Southern hemispheres (Figure S1.8).

3.4 | Cross-Specialisation Patterns

Overall, aridity negatively influenced avian specialisation across all facets (diet, climate and habitat), even after accounting for species richness and spatial autocorrelation (Figures 3 and 4, Table 1). Climate stability showed a moderate negative effect on habitat specialisation but exhibited a smaller influence on diet and climate specialisation. Species richness had a consistently positive effect on diet and climate specialisation, while evolutionary age primarily influenced habitat specialisation.

Lastly, realm-specific models supported the observed contrasting effects of aridity and species richness on bird specialisation in realms from the Northern and Southern hemispheres, emphasising the idiosyncrasy of Northern versus Southern realms.

4 | Discussion

Unravelling what factors drive and maintain ecological specialisation at broad scales is key to understanding the processes that shape biodiversity and community structure across the globe. In this study, we dissect the biogeography of avian specialisation from a multifaceted perspective. By examining different axes of specialisation (climate, diet and habitat) in relation to environmental proxies and biotic factors, we aim to test whether specialisation at the assemblage

TABLE 1 | Environmental predictors of bird specialisation.

Formula	R^2	AIC	Phi ± SE	Intercept ± SE	Estimate ± SE	df
Diet ~ lat	**0.258**	**−71,286**	**204.06 ± 2.30**	**1.999 ± 0.004**	**−0.534 ± 0.007**	**15,728**
Diet ~ lon	0.082	−67,787	163.25 ± 1.84	1.853 ± 0.005	−0.289 ± 0.008	15,728
Diet ~ Richness	**0.401**	**−74,118**	**244.35 ± 2.75**	**1.486 ± 0.003**	**1.005 ± 0.011**	**15,728**
Diet ~ Aridity	0.157	−69,106	177.58 ± 2.00	2.656 ± 0.018	−1.054 ± 0.020	15,728
Diet ~ CSI	0.085	−67,854	163.94 ± 1.85	1.389 ± 0.008	0.463 ± 0.012	15,728
Diet ~ Age	0.187	−69,584	183.02 ± 2.06	2.901 ± 0.021	−2.408 ± 0.042	15,728
Diet ~ Realm	**0.657**	**−82,671**	—	—	—	**15,724**
Habitat ~ lat	0.070	−52,909	81.40 ± 0.91	1.098 ± 0.006	0.328 ± 0.010	15,728
Habitat ~ lon	0.139	−54,062	87.60 ± 0.98	1.530 ± 0.006	−0.440 ± 0.009	15,728
Habitat ~ Richness	0.004	−51,831	76.00 ± 0.85	1.307 ± 0.004	−0.117 ± 0.016	15,728
Habitat ~ Aridity	0.057	−52,695	80.30 ± 0.90	1.986 ± 0.024	−0.769 ± 0.026	15,728
Habitat ~ CSI	0.144	−54,262	88.75 ± 1.00	1.781 ± 0.010	−0.754 ± 0.015	15,728
Habitat ~ Age	0.089	−53,167	82.74 ± 0.93	0.261 ± 0.028	2.041 ± 0.056	15,728
Habitat ~ Realm	**0.353**	**−58,825**	—	—	—	**15,724**
Climate ~ lat	**0.389**	**−39,862**	**50.97 ± 0.57**	**0.861 ± 0.006**	**−1.014 ± 0.010**	**15,728**
Climate ~ lon	0.074	−33,491	34.00 ± 0.38	0.523 ± 0.007	−0.430 ± 0.012	15,728
Climate ~ Richness	**0.281**	**−37,372**	**43.52 ± 0.49**	**−0.001 ± 0.004**	**1.363 ± 0.018**	**15,728**
Climate ~ Aridity	0.050	−33,081	33.13 ± 0.37	1.131 ± 0.030	−0.928 ± 0.033	15,728
Climate ~ CSI	0.117	−34,202	35.57 ± 0.40	−0.269 ± 0.013	0.842 ± 0.019	15,728
Climate ~ Age	0.106	−34,026	35.18 ± 0.39	1.791 ± 0.035	−3.007 ± 0.070	15,728
Climate ~ Realm	**0.778**	**−55,810**	—	—	—	**15,724**

Note: Relationship between climate, diet and habitat specialisation, and a set of explanatory variables across bird assemblages in 15,731 terrestrial grid cells, comprising 9709 species. Single-predictor beta regression models assess the relative importance of each variable. Reported metrics include pseudo-R^2, AIC, degrees of freedom, regression estimate, intercept, precision (phi) parameter and standard errors (SE). Higher phi indicates lower variance. Due to the large sample size ($n = 15{,}729$), all p-values were < 0.001. Age = evolutionary age; lat = latitude; lon = longitude. Estimates are on the log-odds scale; values $> \pm 0.7$ approximate a doubling or halving of odds. Variables explaining > 20% of variance are highlighted in bold.

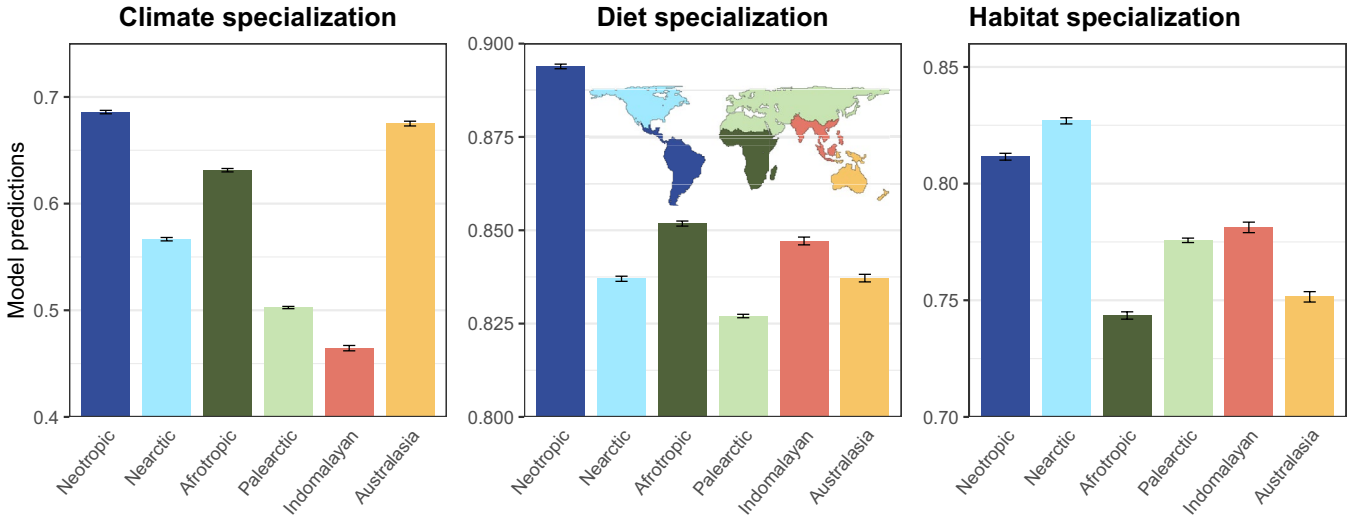

FIGURE 2 | Bird specialisation in different biogeographic realms. Predicted specialisation values in each biogeographic realm using a simple beta regression model (specialisation ~ realm). Error bars represent 95% confidence intervals. Note that the scale on the y-axis varies across panels.

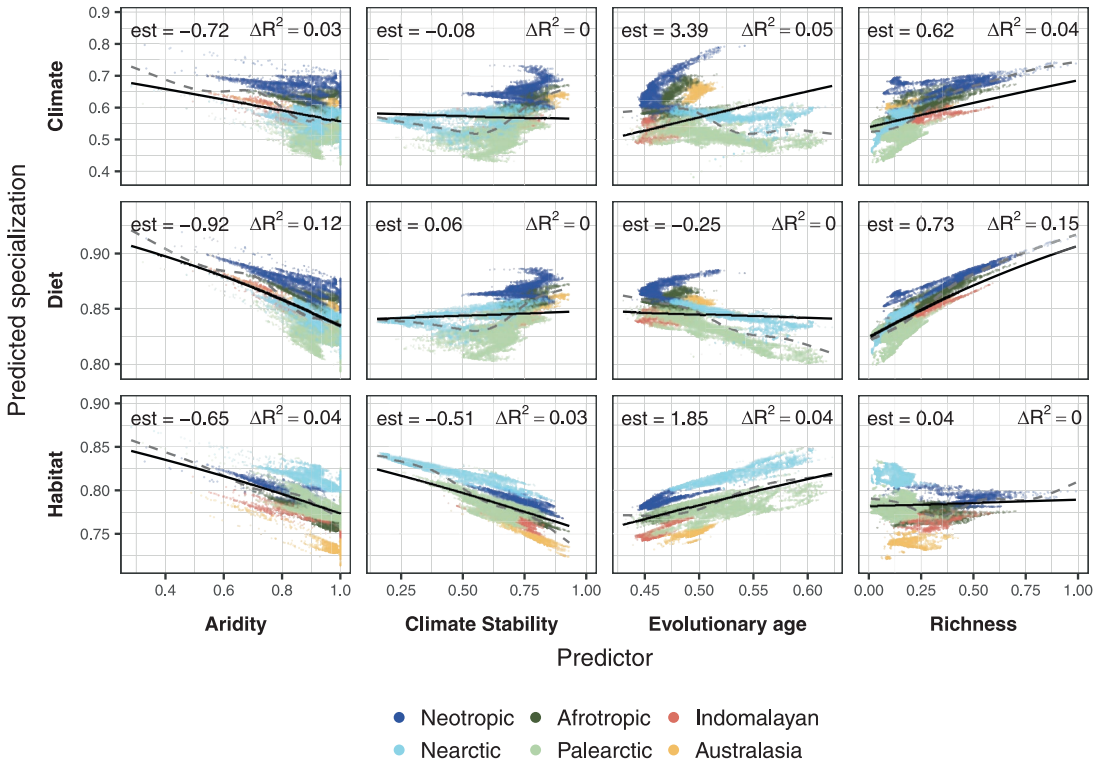

FIGURE 3 | Marginal effects of key predictors on bird specialisation. Marginal effects of aridity, climate stability, evolutionary age and species richness after accounting for spatial autocorrelation. The continuous lines represent the marginal effect of the predictor. ΔR^2 refers to the improvement or diminishment of a specific model pseudo-R^2 compared to the null model with only coordinates (specialisation ~ lat + lon). The dashed lines represent the adjusted generalised additive models (GAMs, $k = 6$), showing that the trend of the linear effect is similar to more complex non-linear effects in most cases.

level can be better explained by current stress-productivity gradients or long-term climate stability, as well as by species richness or evolutionary age. Our findings do not support the climate stability hypothesis in birds and also challenge the notion that more arid environments push species toward specialisation through environmental filtering. Instead, we show that (i) aridity is negatively associated with the three dimensions of specialisation, especially in the Southern Hemisphere (i.e., more benign environments favour specialisation) and (ii) climatic stability was only explanatory for habitat specialisation, suggesting less specialised assemblages in more stable climates. As for the other variables, we observed that species richness is strongly associated with dietary specialisation, while the average evolutionary age of the species in the assemblage can predict habitat and climate specialisation, suggesting the influence of long-term evolutionary processes.

Regarding the effect of species richness, it was positively associated with both dietary and climate specialisation, being the variable that best explained the degree of specialisation in terms of diet. These results are consistent with previous studies (Belmaker et al. 2012; Granot and Belmaker 2020; Pellissier et al. 2018) and suggest that biotic interactions and niche-packing within species-rich communities may play a major role in shaping diet specialisation across the globe (Pellissier et al. 2018). This, and the fact that evolutionarily older assemblages showed less diet specialisation, reinforces the idea that high species richness is mainly associated with a denser occupation of the niche space, leading to increased specialisation in terms of feeding strategies to reduce intraspecific competition (Pigot et al. 2016). The existence of a positive relationship between species richness and climate specialisation may imply that climatically moderate regions (i.e., tropics), which are the ones where more species accumulate, also host more specialised species (i.e., species with narrower climatic niches). Meanwhile, realms in the Northern Hemisphere are poorer in species, and these species can cope with wider temperature and precipitation fluctuations and have wider ranges. This accumulation of narrow-ranged species near the equator has often been proposed as the main reason why species richness increases toward the tropics (e.g., Ghalambor et al. 2006). Taking into account that the tropics constitute the most likely origin for a large number of avian families, such a pattern suggests that the colonisation of environments moderately different from the ancestral one implies the acquisition of a broader climatic tolerance. In this context, studies on other taxa have revealed that species richness progressively declines along a gradient from ancestral to derived climatic conditions, and, in turn, this gradient was negatively correlated with niche breadth (García-Navas and Rodríguez-Rey 2019).

Aridity, used as a proxy for the stress-productivity gradient, showed a negative association with the three facets of specialisation even after accounting for latitude, longitude and species richness. This finding leads us to reject the hypothesis that arid, low-productivity conditions promote specialisation in birds in a generalised manner. Rather, our results suggest the opposite: that primary productivity (i.e., benign environmental conditions) fosters avian specialisation, leaving a strong imprint

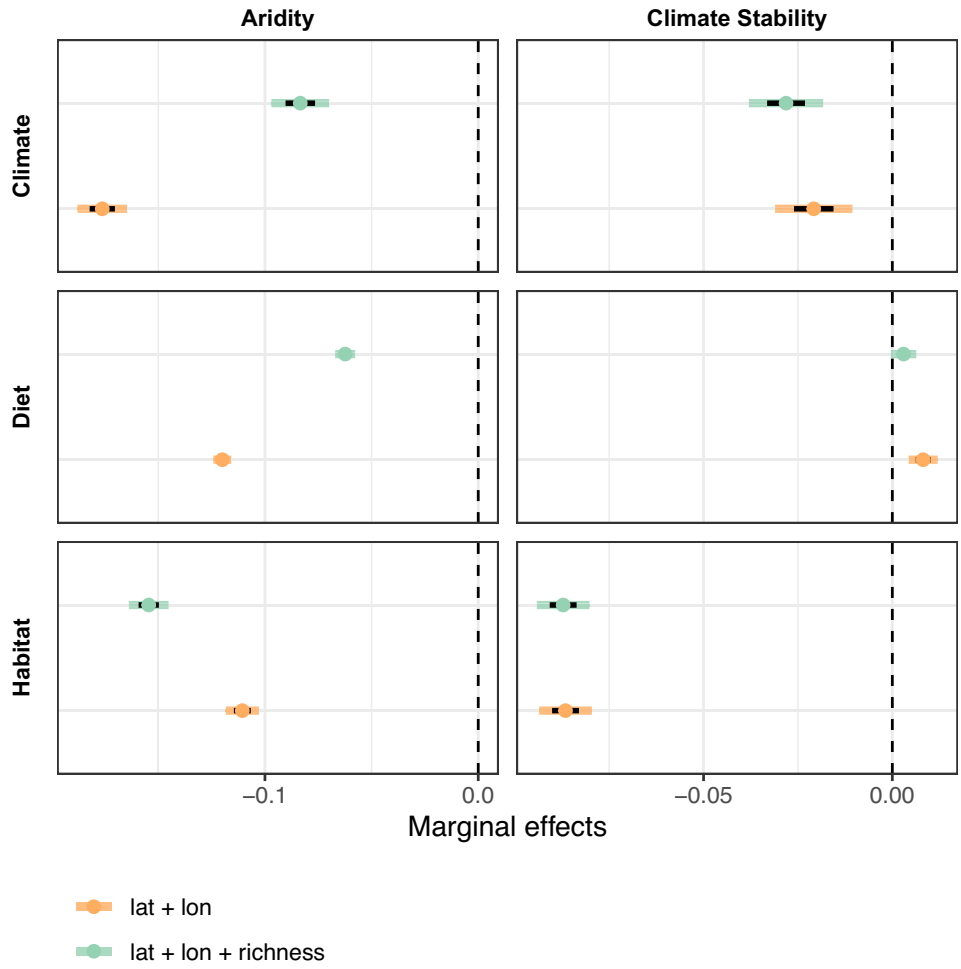

FIGURE 4 | Effects of aridity and climate stability on bird specialisation facets. Marginal effects of aridity and climate stability on climate, diet and habitat specialisation, after accounting for spatial autocorrelation (lat = latitude; lon = longitude) (orange) and autocorrelation and species richness (green). The black bars represent the standard error. The coloured bars represent the 95% confidence interval.

detectable at the regional assemblage level. In this vein, Wiens et al. (2013) reported that reptile species in arid environments often exhibit broader niche breadths, challenging the assumption that extremely arid conditions consistently drive specialisation. While the relationship between specialisation and environmental stress has been extensively explored in studies on stress-productivity gradients in plants (e.g., Boulangeat et al. 2012), it has been barely explored in animals. A notable exception is Rivas-Salvador et al. (2019), who showed that European bird communities settled in areas with more extreme climatic conditions showed greater specialisation. Our findings generally align with Rivas-Salvador et al. (2019) as the Palearctic realm exhibited an overall positive (but weak) association between aridity and specialisation. A possible explanation for this result is that in the Palearctic, arid environments coincide with historical hotspots of biodiversity, such as the Mediterranean basin, hosting rich communities where specialising in specific resources might increase species' competitive potential and fitness (Blondel et al. 2010). Yet, this trend seems to be idiosyncratic of the Northern Hemisphere, as we observed negative aridity-specialisation associations for all the southern realms. Our results thus indicate that, at a global scale, processes leading to bird specialisation are stronger in benign conditions (non-arid, highly productive habitats) rather than in arid and harsh environments where facilitation interactions prevail over competitive ones (e.g., García-Navas et al. 2023).

Concerning past climatic conditions, it is often expected that regions with stable climates harbour more specialised species due to long-term ecological stability; whereas unstable climates (e.g., regions affected by glaciations or extreme seasonal variation) create frequent disturbances that favour generalist species (i.e., those that can exploit a wide range of resources and adapt to fluctuating conditions) and make specialists more likely to go extinct because they cannot adapt quickly to changing conditions (R. H. MacArthur 1972; Rodrigues-Filho et al. 2018). Our findings, however, do not support this hypothesis. The CSI was a weak predictor of specialisation, showing limited explanatory power even as a single predictor despite its strong correlation with latitude. Notably, it only provided a substantial explanation for habitat specialisation, indicating the existence of lower specialisation (i.e., broader ecological tolerance) in climatically stable regions. This aligns with meta-analyses including multiple taxa, which have shown that climatic stability alone does not consistently drive specialisation (Granot and Belmaker 2020; Vázquez and Stevens 2004). The weak (and even negative in some cases) effect of climate stability on bird specialisation may be partly attributed to birds' high dispersal capacity,

which allows them to exploit a variety of environments and resources across stable regions, further diminishing the need for specialisation in comparison with less mobile organisms (e.g., Rodrigues-Filho et al. 2018).

In addition, our results indicate that the biogeographic realm to which each assemblage belongs largely determines their level of specialisation for each of the three axes, suggesting that idiosyncratic legacy effects and the particular evolutionary history of each biogeographic region have a meaningful impact on the width of the niche exploited by each bird species (Kissling et al. 2012). In this sense, the Neotropics showed the highest overall specialisation, possibly due to an expansion of the available niche space toward the tropics, where greater habitat complexity and energy availability, along with a relaxation of the biophysical constraints imposed by cold or highly seasonal environments, lead to an increased volume and density of functional trait space (see Lamanna et al. 2014; Pigot et al. 2016). This scenario would have spurred the diversification of the Tyrannoidea superfamily, one of the largest avian radiations whose members show remarkable ecological diversity and have colonised a wide range of habitats throughout the American realms (Belmaker et al. 2012; Ohlson et al. 2008). On the opposite end of the spectrum, we find the case of the Afrotropic realm, which exhibited the lowest value of habitat specialisation. It is unlikely that this result is due to a biased habitat classification, as the distribution of habitats across realms was relatively uniform. The existence of a low degree of habitat specialisation in the Afrotropic realm might reflect the region's dynamic environmental history, where recurrent climatic fluctuations, forest retractions and savanna expansions in the Pliocene likely favoured generalist strategies over specialisation (Voelker et al. 2010). In addition, the relatively recent diversification of several bird lineages with broad ecological niches like bulbuls (Pycnonotidae) or bush-shrikes and allies (Malaconotidea) might have favoured a low habitat specialisation in the Afrotropic realm (Fjeldså and Bowie 2008; Fuchs et al. 2012).

Lastly, we observed evidence for the role of evolutionary history in shaping specialisation patterns. Older assemblages exhibited greater habitat and climatic specialisation, which may be because some non-passeriform groups—which are evolutionarily old and represent basal lineages within the avian phylogenetic tree—have specialised to thrive in unique habitats and extreme environments (Antarctic ice sheet, deserts, cliffs) where Passeriformes (the largest and one of the youngest avian orders) are less common (Fjeldså et al. 2020). Notably, this global pattern was mainly driven by the Nearctic and Palearctic realms, where the proportion of non-Passeriformes is lower in comparison with Africa or Australasia. However, in terms of biodiversity, these are the most species-poor realms, whereas the Neotropic realm exhibits the greatest number of bird species. Specifically, tropical rainforests are home to the greatest diversity of perching birds whose explosive and relatively recent radiation probably originated in this region, in which speciation rates tend to be higher (Jetz et al. 2012; Fjeldså et al. 2020). In this sense, it has been reported that higher rates of lineage diversification are associated with higher rates of climatic niche evolution (e.g., Title and Burns 2015), which may explain the existence of higher levels of climatic and habitat specialisation in speciose and evolutionarily recent clades like tanagers (Thraupidae), waxbills and allies (Estrildidae), or vireos (Vireonidae). Consequently, younger lineages may evolve narrower climatic niches due to selective pressures favouring ecological divergence from ancestral conditions, especially during rapid radiations or in environments with high species density (Pigot and Tobias 2013; Skeels and Cardillo 2019). Thus, the existence of opposite trends in realms from the Northern and Southern Hemispheres could reflect distinct evolutionary pressures, where old glaciation events and historically less diverse assemblages in the Northern Hemisphere may have shaped different paths of specialisation. In the Southern Hemisphere, realms like the Neotropics show high habitat diversity and have experienced relatively stable climates, which, coupled with the effect of geographic barriers like the Andean cordillera or the Amazon, may have promoted rapid diversification and specialisation in relatively recent radiations (Fjeldså et al. 2020).

While our study offers insights into global patterns of avian specialisation, it is important to consider the implications of using a relatively coarse spatial resolution (1° grid cells). Although this resolution is well-suited for identifying broad biogeographic and evolutionary patterns and has been widely used in global studies, it may smooth or amplify certain relationships. Some scale-dependent processes may manifest differently at finer resolutions. For example, Belmaker et al. (2012) showed that the richness–specialisation relationship appeared steeper at coarser scales, whereas associations with environmental variables like aridity might be more pronounced at finer grains, particularly if specialists respond to microhabitat variation. Thus, while our findings are robust at the regional-to-global scale, covering wide ranges in environmental variables, finer-scale studies could complement our results by revealing localised mechanisms of specialisation.

In conclusion, our study shows that current stress-productivity gradients, species richness and evolutionary history play a more significant role in shaping global specialisation patterns than long-term climatic stability. These findings do not support the prevailing hypothesis, which posits that long-term climate stability leaves a lasting imprint on the specialisation of contemporary bird assemblages. In addition, our results do not reinforce the idea that stressful environments inherently promote specialisation. Instead, our study suggests that worldwide specialisation patterns in birds are primarily driven by processes associated with high productivity conditions, where species diversity tends to peak and where most young lineages accumulate. This indicates that niche filling mechanisms exert a strong influence on the urge of species to exploit narrower niches. Given the role of productivity in fostering specialisation, our findings highlight the importance of protecting high-productivity habitats to sustain both specialised species and the broader processes that drive specialisation.

Acknowledgements

We are grateful to Federico Morelli for sharing the data regarding diet specialisation and his constructive comments. We also appreciate the comments and feedback provided by Martina Carrete, Duarte Viana and Pedro Romero-Vidal. R.M. was supported by a JAE Intro-CSIC internship (JAEINT_23_02188). C.M.N. was supported by the 'Juan de la Cierva' programme (ref. FJC2021-046829-I). V.G.N. received funding from Agencia Estatal de Investigación (grant ref. CNS2023-144066).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data and code of this study are publicly available in Figshare: https://figshare.com/s/63e980ee3bdaf6f0fd0e (DOI: 10.6084/m9.figshare.28347353).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1.** Correlations, sensitivity analyses and model parameters. **Table S1.1.** Beta regression parameters with spatial autocorrelation. **Figure S1.1.** Climate specialisation sub-index predictions by realm. **Figure S1.2.** Marginal effects on climate specialisation. **Figure S1.3.** Climate specialisation with

and without migrants. **Figure S1.4.** Marginal effects on climate specialisation (full model). **Figure S1.5.** Pairwise correlations of explanatory variables. **Figure S1.6.** Residual diagnostics for beta regression models. **Figure S1.7.** Model predictions by realm for all predictors. **Figure S1.8.** Marginal mean effects across all predictors. **Appendix S2.** Sensitivity analysis for habitat specialisation. **Figure S2.1.** Habitat dissimilarity based on Jaccard index. **Figure S2.2.** Shared species percentages between habitats. **Figure S2.3.** Dendrogram of habitat type dissimilarities. **Figure S2.4.** Maximum shared species among habitat types. **Figure S2.5.** Habitat area percentages per realm. **Table S2.1.** IUCN-based habitat category inclusion. **Table S2.2.** Habitat reclassification criteria. **Table S2.3.** Beta regression parameters for habitat specialisation.