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Biome Specialisation in Squirrels: Phylogenetic and Geographic Patterns

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ABSTRACT

Aim: Habitat breadth shapes species' responses to environmental change and influences large-scale biodiversity patterns. According to Vrba's resource-use hypothesis, biome specialists (inhabiting a single biome) exhibit higher speciation rates than generalists due to increased population isolation during habitat fragmentation, generally associated with past climate changes, particularly in biomes at extremes of the global climatic gradient. However, the phylogenetic and geographic distribution of biome specialists remains poorly understood. Here, we use squirrels to assess whether: (1) clades accumulate more specialist species than expected by chance, (2) this accumulation is associated with biomes at the extremes of the climatic gradient (tropical rainforest, subtropical desert, steppe and tundra), (3) habitat specialisation relates to geographic patterns of phylogenetic diversity and (4) species-level recent speciation rates.

Location: Global.

Taxon: Squirrels (Sciuridae, Rodentia).

Methods: We compared observed biome specialisation indices (BSI) of species to MCMC-generated null distributions. We then mapped global patterns of specialist and generalist richness, phylogenetic diversity and recent species-level speciation rates.

Results: Squirrels include more biome specialists than expected under a null model that randomises biome occupancy, supporting the resource-use hypothesis. Tropical rainforests and steppes harboured more specialists than expected, whereas deserts and tundra did not, the latter likely due to their low species richness. Regions with high specialist richness (e.g., Southeast Asia) exhibited lower levels of phylogenetic diversity, consistent with Miocene speciation. In contrast, high recent speciation occurred in Holarctic steppes and South America, likely reflecting Pleistocene glacial radiations and post-Panamanian colonisation, respectively.

Main Conclusions: During periods of climatic change, the origin of new specialist lineages through rapid speciation led to specialist-dominated and phylogenetically clustered faunas, particularly in fragmented biomes. However, recent speciation rates

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reflect emerging rather than historical diversification hotspots. The Sunda Shelf emerges as a key conservation priority due to its exceptional richness, low phylogenetic diversity and concentration of endemic specialists.

1 | Introduction

Habitat breadth is defined as the range of environments over which species occur (Pyron 1999; Harnik et al. 2012; Nürnberg and Aberhan 2013; Ducatez et al. 2014). Some species are widely distributed across different environmental conditions, while others are environmentally specialised and have narrow habitat breadths. How many distinct environments a species can occupy mediates species' responses to environmental changes, shaping large-scale patterns of biogeography and species richness (Slatyer et al. 2013; Carscadden et al. 2020). Yet, even after several decades of research, the evolutionary implications of ecological specialisation and how it shapes biodiversity patterns remain under investigation (Futuyma and Moreno 1988; Brown and Pavlovic 1992; Hernández Fernández and Vrba 2005b; Jocque et al. 2010; Belmaker et al. 2012; Vamosi et al. 2014; Nürnberg and Aberhan 2015; Auffret et al. 2017; Mills et al. 2020; Fargallo et al. 2022; Padfield et al. 2024; Gamboa et al. 2025).

For instance, habitat specialisation has often been proposed to represent an evolutionary dead end, as specialists are expected to have reduced geographic ranges, fewer opportunities for habitat shifts, and consequently higher extinction risk (Futuyma and Moreno 1988; Vamosi et al. 2014; Day et al. 2016). However, specialisation has also been invoked as a promoter of speciation by reducing gene flow: because specialists have narrower environmental ranges and more fragmented distributions, they may be more prone to allopatric divergence than generalists (Fryer and Iles 1969; Futuyma and Moreno 1988). Moreover, several studies have reported diversification differences that are not straightforwardly explained by shifts in niche breadth (Hardy and Otto 2014; Gómez-Rodríguez et al. 2014), while others suggest that both speciation and extinction rates can be higher in specialised lineages (e.g., Vamosi et al. 2018).

Within this debate, and congruently with these latest findings, Vrba's Habitat Theory provides a mechanistic framework. In particular, the Resource-Use Hypothesis proposes that habitat specialisation modulates evolutionary outcomes under environmental change by increasing diversification in habitat specialists (Vrba 1980, 1987, 1992, 1993). When habitats fragment due to climatic shifts, species confined to a single habitat are more likely to experience range fragmentation, as they usually track their habitat. This might lead to evolutionary divergence among populations when the fragments are sufficiently isolated to limit gene flow. This could produce extinction (if effective population sizes collapse) or allopatric speciation (if isolated populations persist), influencing their diversification rates. In contrast, broad-habitat generalists are expected to maintain more continuous ranges and thus exhibit more muted responses in speciation and extinction rates. Consequently, although extinction rates of habitat specialists may be high during episodes of pronounced global change, once conditions stabilise, speciation within surviving lineages is predicted to generate new specialist species, increasing the proportion of specialists in the biota over time (Vrba 1992, 1993).

Within Vrba's Habitat Theory, other connected hypotheses have received considerable attention (see Faith et al. 2024 for a summary of conflicting results for the Turnover-Pulse hypothesis in the African mammalian fossil record). By comparison, the Resource-Use Hypothesis has been less frequently and less explicitly tested, although available evidence is often consistent with its predictions. In Pliocene rodents from the Iberian Peninsula, there was a decrease in the specialisation degree due to a global cooling event, a pattern consistent with high extinction of specialists during environmental crises (Gómez Cano et al. 2013). Studying extant clades, several studies report a higher proportion of biome specialists than expected by chance, a pattern consistent with elevated speciation in specialists when it exceeds extinction after climatic change crises (Hernández Fernández and Vrba 2005a; Moreno Bofarull et al. 2008; Cantalapiedra et al. 2011; Gamboa et al. 2022; Hernández Fernández et al. 2022; Pelegrin et al. 2023; Thomas et al. 2024). This pattern has been found especially in those environments that have undergone a high degree of fragmentation associated with global climatic changes, such as biomes located at the extremes of the temperature and precipitation gradient, which are likely to experience greater fragmentation during climatic change events (Hernández Fernández and Vrba 2005a; Cantalapiedra et al. 2011; Gamboa et al. 2022; Hernández Fernández et al. 2022; Pelegrin et al. 2023). Further, trait-dependent analyses also suggest higher diversification in specialists for ruminants (Cantalapiedra et al. 2011), squirrels (Menéndez et al. 2021) and butterflies (Gamboa et al. 2022).

However, key predictions derived from the Resource-Use Hypothesis have not yet been fully explored. If specialist species originate more frequently in particular environments, we would expect heterogeneous geographic patterns of specialist richness, with some regions disproportionately enriched in specialists. Furthermore, if specialists exhibit both high speciation rates and high niche conservatism (Peterson et al. 1999; Wiens 2004; Crisp et al. 2009; Cooper et al. 2011; Rolland and Salamin 2016; Resl et al. 2018; He et al. 2023; Pelegrin et al. 2023; Qiao et al. 2024), regions with a higher proportion of specialists should show phylogenetic clustering (i.e., lower phylogenetic diversity, once corrected for species richness) and elevated recent speciation rates. However, despite the theoretical support, the geographical distribution of biome specialists and its relationship with geographic patterns of phylogenetic diversity and speciation rates has not been thoroughly addressed. This relationship could have important implications for conservation, as regions with low phylogenetic diversity may still be a priority to protect due to their high concentration of specialists—species more prone to extinction—and their potential as future hotspots of diversity.

This work aims to explore the distribution of biome specialists across clades, biomes, and geography in squirrels (Sciuridae, Rodentia). This lineage of rodents is very diverse and globally distributed, occurring in all terrestrial biomes and almost all continents (Thorington et al. 2012; Koprowski et al. 2016). Moreover, previous analyses support a central prediction of the Resource-Use Hypothesis in this group: biome specialists have higher speciation rates than biome generalists under a trait-dependent framework (Menéndez et al. 2021). This makes the squirrel family an excellent model to test whether (1) elevated speciation in specialists leads to an accumulation of specialist species within the clade; and (2) this accumulation is enhanced in biomes located at the extremes of the global climatic gradient of temperature and precipitation (i.e., tropical rainforest, subtropical desert, steppe and tundra). Additionally, we explored the geographical patterns of species based on their biome specialisation, and the geographic distribution of phylogenetic diversity and species-level speciation rates, to understand how habitat breadth contributes to the diversity patterns that we observe today. Under the Resource-Use Hypothesis, we would expect (3) low phylogenetic diversity in regions with a high number of specialist species and (4) high speciation in regions with more specialist species. Finally, we assess the implications of these findings for conservation, highlighting regions of high specialisation that may be particularly vulnerable to environmental changes.

2 | Material and Methods

2.1 | Biome Occupancy

We used the dataset from Menéndez et al. (2021), in which biome occupancy for all modern squirrel species ($n = 292$) was assessed by comparing their global distribution (Koprowski et al. 2016) with the distribution of world biomes following Walter's (1970) classification, modified to include the distinctive savannah ecotone as in Hernández Fernández (2001) (Figure 1). A species was considered to occupy a biome following a two-fold criterion (Hernández Fernández 2001): when at least 15% of its geographical range was included within a biome or when it inhabited at least 50% of one climatic dominion, which is a continuous terrestrial area of one biome only (Figure 1). This two-fold criterion allows us to accurately categorise species with very large geographic ranges, whose complete occupancy of a small dominion might not reach 15% of their distributions. The altitudinal gradient was also considered when categorising species into biomes; mountain vegetation belts were treated as their analogous latitudinal biomes since they present very similar climatic conditions, vegetation physiognomy and fragmentation dynamics during climatic fluctuations (Hernández Fernández and Vrba 2005a; Moreno Bofarull et al. 2008; Cantalapiedra et al. 2011; Hernández Fernández et al. 2022).

We also obtained the biome specialisation index (BSI) for each species from Menéndez et al. (2021). BSI represents the number of biomes it occupies (Hernández Fernández and Vrba 2005a). Following Hernández Fernández and Vrba (2005a) we classified species as specialists when they occurred in a single biome ($\mathrm{BSI} = 1$) and as generalists when they occupied more than one biome. Consistent with previous macroevolutionary studies, we further distinguished between moderate generalists ($1 < \mathrm{BSI} < 5$) and extreme generalists ($\mathrm{BSI} \geq 5$), as species in the latter category necessarily span biomes that are climatically and structurally highly dissimilar, reflecting exceptionally broad ecological tolerance (Hernández Fernández and Vrba 2005a).

2.2 | Proportion of Specialist Species in Clades and Biomes

We tested in squirrels Vrba's predictions (Vrba 1980, 1987) that specialist species accumulate more than expected by chance (1) within clades and (2) within biomes located at the extremes of the global climatic gradient of temperature and precipitation. To do so, we compared the observed number of squirrel specialists with expectations derived from a null model (1) across the whole family Sciuridae and subfamilies with more than 10 species, and (2) across biomes. We built this null model with 10,000 Markov Chain Monte Carlo (MCMC) permutations of the biome presence-absence matrix. In all permutations, we constrained the squirrel species richness of each biome to preserve biome-specific carrying capacities (Hernández Fernández and

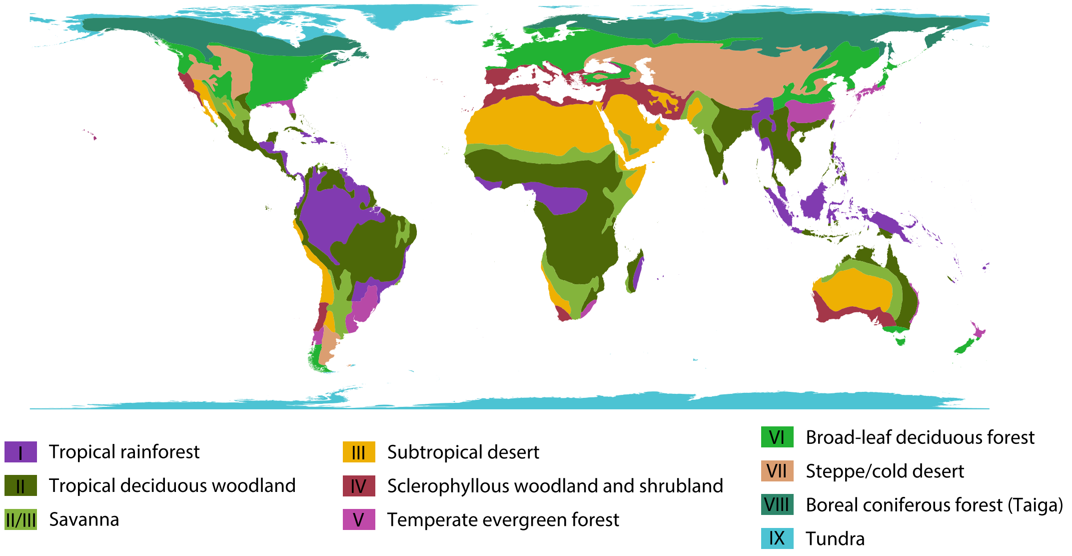

FIGURE 1 | Biome distribution used in this work and corresponding vegetation types in the world (modified from Walter 1970, and Allué Andrade 1990). Dominions are the different areas of the same biome (e.g., the steppe biome, here coloured in light brown, is divided into different dominions in western North America, southern South America and central Eurasia).

Vrba 2005b; Cantalapiedra et al. 2011), accounting for differences among biomes related to geographic area, resource availability and other factors associated with carrying capacity. In each permutation, we recorded the number of biomes occupied by each species (BSI) and the number of specialists present in each biome. Using the resulting null distributions, we assessed the probability (p-value) of obtaining the observed BSI proportions within clades (family and subfamilies) and the proportion of specialists (BSI = 1) across biomes (Gotelli 2000).

2.3 | Lineage Recent Speciation Rates

To explore the geographic patterns of speciation, we quantified a species-specific metric of speciation rates (DR metric; Jetz et al. 2012). Due to the difficulties of estimating extinction rates and historical diversification dynamics from extant-species phylogenies, tip rates are the best metric that we can obtain from extant time-trees (Rabosky 2016; Louca and Pennell 2020) and provide a useful species-specific metric to study diversification in relation to geography at multiple scales (Jetz et al. 2012; Title and Rabosky 2019).

The DR metric is calculated as the inverse of the species' equal splits (ES) value. ES quantifies the branch lengths along the path from the root to the tip of a phylogeny, assigning greater weight to branches closer to the present (Redding and Mooers 2006; Jetz et al. 2012). Species with larger contributions of recent branch lengths have lower ES values and therefore higher DR values. Although DR was initially used as a measure of species-specific diversification rate (Jetz et al. 2012), subsequent work has shown that it more accurately reflects recent speciation rather than net diversification (Title and Rabosky 2019).

We estimated the DR metric using the function DRstat from *epm* package (Title et al. 2022). To account for phylogenetic uncertainty, we calculated DR across 100 posterior phylogenies of extant squirrels and then computed the mean DR value for each species. To obtain DR estimates for all recognised Sciuridae species, we used 100 posterior trees of the most up-to-date molecular squirrel phylogeny (225 species) as a backbone (Menéndez et al. 2021) and incorporated the 67 species lacking molecular data using the taxonomy-based TACT method (Chang et al. 2020). These 67 species (listed in Data S1) were randomly placed at the genus level independently in each posterior tree. The resulting set of 100 trees, which includes all currently recognised Sciuridae species following Koprowski et al. (2016), is provided in Data S2.

2.4 | Geographic Patterns

To explore geographic patterns of specialisation independently of biome-level comparisons, we conducted a grid-based spatial analysis of squirrel diversity worldwide. To do that, we created global maps of the total richness, richness of specialists (BSI = 1), moderate generalists ($1 < \text{BSI} < 5$), and extreme generalists ($\text{BSI} \geq 5$), to visually explore geographic patterns of squirrel diversity and how species with different degrees of specialisation contribute to them. To do that, we used the available squirrel polygon distribution data ($n = 277$) from IUCN Red List (IUCN 2018) to generate raster files with a resolution of 50 × 50 km using the *epm* R package (Title et al. 2022). This package calculates community metrics for each cell in a grid (raster), enabling the mapping of these metrics in a geographic context. This grid size is appropriate for global studies of species richness, consistent with the spatial precision of IUCN range data, and widely used in macroecological research. Additionally, we explored the percentage of specialists, moderate generalists, and extreme generalists species in each cell and surveyed the composition of grid-cell assemblages regarding phylogenetic relationships through Faith's phylogenetic diversity (PD; Faith 1992), which is calculated as the sum of the branch lengths in the minimum spanning path of the species present in every cell. This allowed us to distinguish between regions with closely and distantly related species. Because there is a strong relationship between phylogenetic diversity and species richness (Davies and Buckley 2011; Voskamp et al. 2017), we also mapped the richness-corrected phylogenetic diversity (residual PD) and explored its relationship with specialists' richness. Moreover, in order to identify regions where species are currently speciating, we also calculated the mean tip rates (DR) of the species present in each cell. Code to produce these maps is provided in Code S1.

3 | Results

3.1 | Specialisation Among Clades

The distribution of BSI among all Sciuridae is strongly right-skewed (Figure 2), with over half of the species inhabiting either one (37.3%) or two biomes (37.3%). The mean of observed BSI is very low (BSI = 2), and none of the species reached a BSI higher than seven, which implies extremely high bioclimatic tolerance. We found a significantly higher percentage of specialist species (BSI = 1) than expected by the null model, which randomly permuted species' biome occurrences while preserving biome-specific richness (Figure 2, Table S1). We also found a significantly higher proportion of species inhabiting five biomes than expected. Conversely, the number of species inhabiting three and four biomes was significantly lower than that obtained from the MCMC simulations.

Subfamilies with more than 10 species showed similar right-skewed patterns of BSI distribution, with low mean BSI values (Callosciurinae = 1.7, Sciurinae = 2.3 and Xerinae = 2.0). While Callosciurinae showed a higher proportion of specialists (49.3%) compared to Sciurinae (30.3%) and Xerinae (36.6%), all of them showed a significantly higher percentage of specialists than in the simulations (Figure 2, Table S1). In contrast, generalists typically did not differ from random expectations. When differences were observed, moderate generalists were consistently underrepresented, while extreme generalists were overrepresented (Figure 2, Table S1).

3.2 | Specialisation Among Biomes

Tropical rainforest (I) and steppe (VII) were the only biomes showing significantly more specialist species than expected based on the MCMC simulations (Figure 3; Table S2). On the other hand, the observed number of specialist species in the

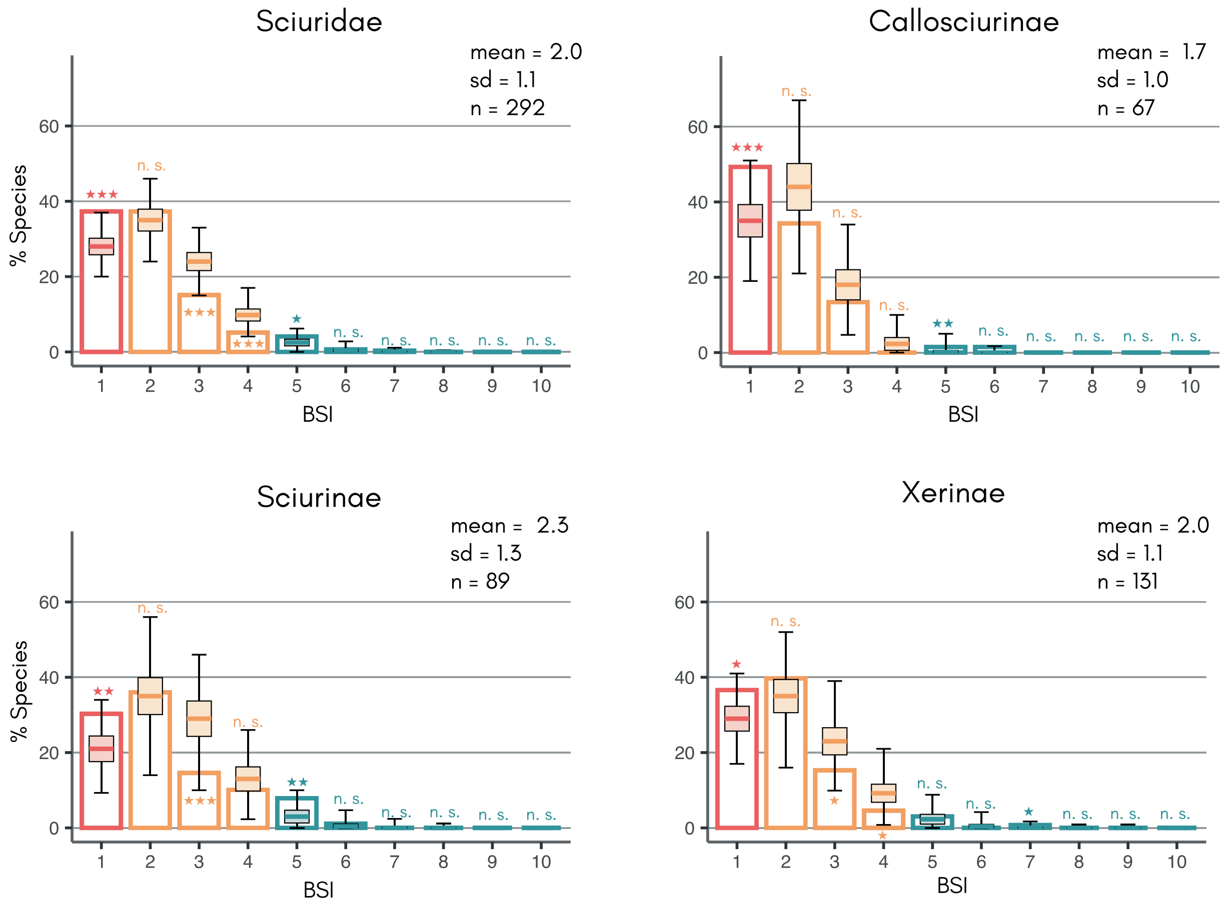

FIGURE 2 | Biome Specialisation Index (BSI) distribution in all Sciuridae and subfamilies Callosciurinae, Xerinae and Sciurinae. Colours indicate the biome specialisation degree: Red = specialist species; yellow = moderate generalist species; blue = extreme generalist species. Boxplots indicate the expected values obtained by MCMC simulations. Significance symbols above or below the boxplots indicate whether observed values are significantly higher (above) or lower (below) than expected by chance; ***$p < 0.001$; **$0.001 < p < 0.01$; *$0.01 < p < 0.05$; ns, not significant. Additional data are provided in Table S1.

temperate evergreen forest (V) was lower than expected according to the null model. The remaining biomes did not show significant differences compared to the expectation derived from chance.

3.3 | Geographical Distribution of Specialisation and Species Richness

In squirrels, regions with higher richness include Southeast Asia, North America, and certain areas in equatorial Africa and South America (Figure 4a). The tropical rainforests and mountainous regions of Southeast Asia provide habitat for numerous squirrel species. Similarly, in North America, particularly in regions such as the eastern and western United States and Canada, several species of squirrels coexist, including chipmunks, marmots and other ground-dwelling squirrels, as well as *Glaucomys* flying squirrels and different tree squirrels (i.e., *Sciurus*, *Tamiasciurus*). Forest and dry woodland areas of central Africa also exhibit notable richness, hosting coexisting tree and ground squirrels from genera such as *Funisciurus*, *Heliosciurus*, *Myosciurus*, *Paraxerus*, *Protoxerus* and *Epixerus*. Additionally, the western regions of the Amazon rainforest show a relatively high richness, with numerous arboreal squirrel species from the genera *Sciurus*, *Microsciurus* and *Sciurillus* cohabiting these environments. The main squirrel hotspot is in Borneo, Sumatra, and the Malay peninsula, where many arboreal (e.g., *Calloscirus*, *Sundasciurus*) and flying squirrels (e.g., *Hylopetes*, *Petinomys*) can be found.

Faith's phylogenetic diversity parallels species richness patterns (Figure 4b), but delving into richness-corrected phylogenetic diversity provides deeper insights (Figure 4c). Comparing the maps, regions with the highest species richness (particularly Sumatra and northern Borneo) tend to show lower residual PD, consistent with phylogenetic clustering. In contrast, regions with lower species richness generally exhibit higher residual PD.

Geographic patterns of recent speciation showed low rates in Africa and in most of Eurasia, except for the central region of Asia (Figure 4d). America showed generally higher rates of speciation, with the highest rates in southwestern US and southeastern Venezuela.

Specialist richness also exhibited a hotspot in southeast Asia (Figure 5a). In the richest region, Borneo, we found up to 27 species, 20 of which are specialists. Although with a much lower number of specialist species, other areas where specialists are relevant include the Rocky Mountains, the Andes and western Amazonas Basin, the Guinean rainforest, Mozambique, and central Asia. We observed a negative relationship between specialist richness and richness-corrected phylogenetic diversity (slope = −3.66; $p < 0.001$; Figure 6), indicating that regions with high diversity of specialists generally harbour more closely related species.

Our results revealed an important percentage of specialists in Borneo (Figure 5b). However, the pattern within the island is inversely related to specialist richness: there is a higher proportion of specialists in the south (Indonesia), but a higher total number of specialist species in the north (Malaysia), although this might be influenced by the discrepancy in research coverage between the Malaysian and Indonesian sides of Borneo. In regions like the steppes of central Asia and specific areas in Colombia and Mozambique, the species pool consists exclusively of specialist species. Moderate generalist species, on the other hand, were more widespread overall (Figure 5c,d). In some regions, such as northern India, Pakistan, central Anatolia, and the arid systems of central Mexico, only extreme generalists were found (Figure 5e,f).

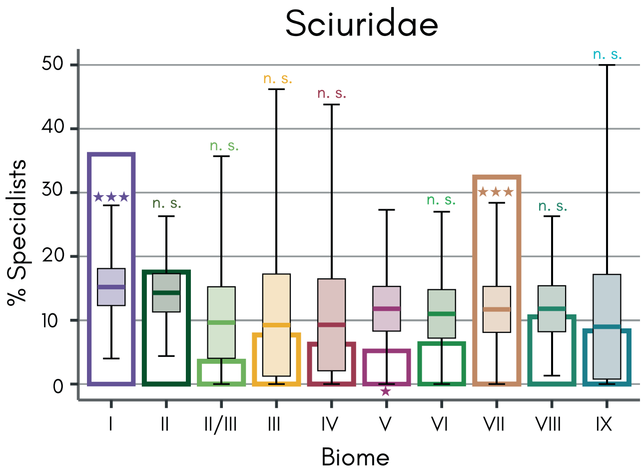

FIGURE 3 | Observed (bars) and simulated (boxplots) percentage of specialists (BSI = 1) squirrel species across different biomes. Significance symbols above or below the boxplots indicate whether results are significantly higher (above) or lower (below) than expected by chance; ***$p < 0.001$; **$0.001 < p < 0.01$; *$0.01 < p < 0.05$; ns, not significant. Colour for biomes corresponds to Figure 1. Additional data are provided in Table S2.

4 | Discussion

We found more specialist squirrel species than expected by chance (BSI = 1; Figure 2), as previous works showed in African large mammals (Hernández Fernández and Vrba 2005a), South American mammals (Moreno Bofarull et al. 2008), ruminants (Cantalapiedra et al. 2011), all terrestrial mammals (Hernández Fernández et al. 2022) and even nonmammalian lineages such as swallowtail butterflies (Gamboa et al. 2022) or testudines (Thomas et al. 2024). This supports our first prediction (1), in which the high levels of specialists are interpreted as a consequence of the higher speciation rates observed in biome specialists (Cantalapiedra et al. 2011; Gamboa et al. 2022) as observed specifically in squirrels (Menéndez et al. 2021). Given the exponential nature of the diversification process, this would have led to a higher relative accumulation of specialist species over time. This is also consistent with the observed relationship between richness-corrected phylogenetic diversity and specialist richness (prediction 3): cells on the map with a high number of specialist species show low levels of phylogenetic diversity (Figure 6). This suggests that intra-group speciation may be the origin of species in regions with a high number of biome specialists. On the other hand, the higher-than-expected frequency of extreme generalist species (BSI ≥ 5) found in some cases (Figure 2) is congruent with results reported generally in mammals (Moreno Bofarull et al. 2008; Hernández Fernández et al. 2022), and may be attributed to lower extinction rates due to their ecological flexibility (Hernández Fernández and Vrba 2005a; Cantalapiedra et al. 2011; Hernández Fernández et al. 2022).

We also found partial support for the Resource-Use Hypothesis prediction related to the increased proportion of specialist species in biomes at the extremes of the global climatic gradient of temperature and precipitation when compared to other biomes

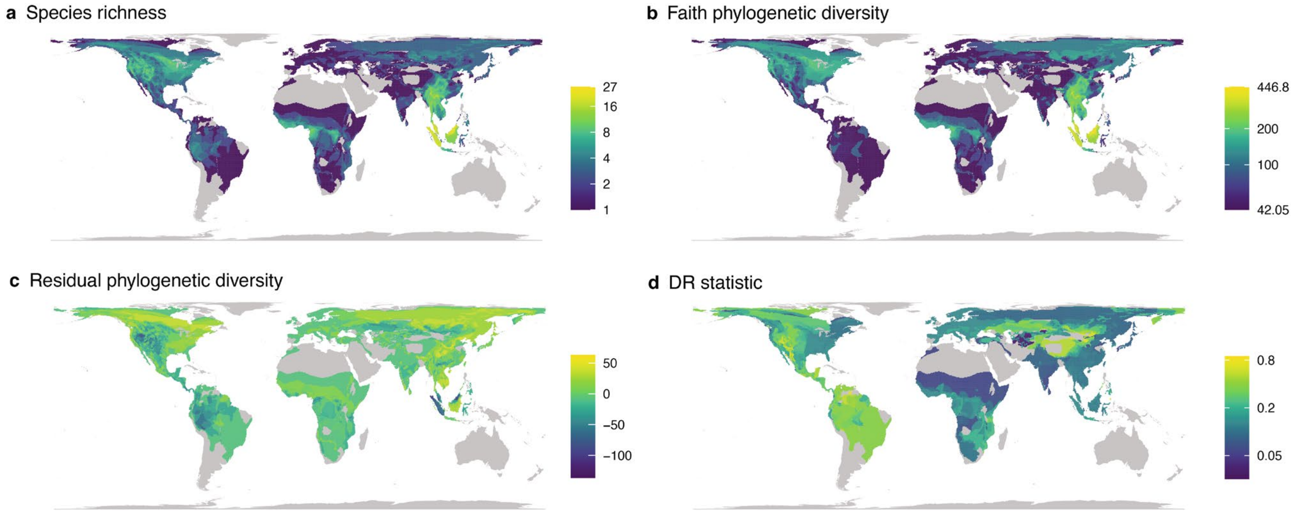

FIGURE 4 | Geographical patterns in the family Sciuridae for (a) Species richness, (b) Faith's phylogenetic diversity, (c) phylogenetic diversity corrected for species richness and (d) recent speciation rate, measured as the DR statistic. Colour gradients are log-scaled.

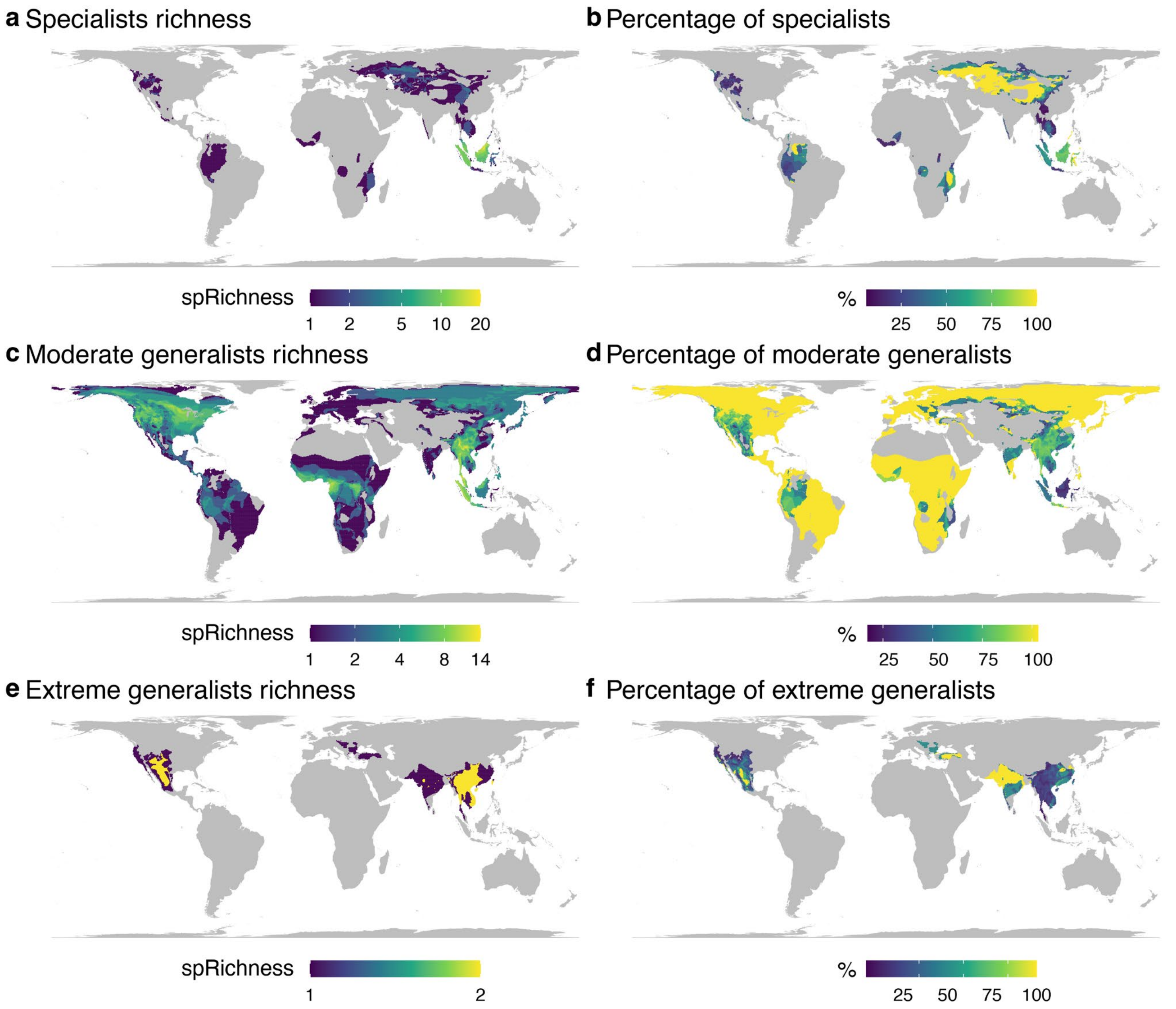

FIGURE 5 | Geographical patterns of specialists, moderate generalists, and extreme generalists' richness (a, c, e, respectively) and percentage of species (b, d, f). Colour gradients are log-scaled.

(prediction 2; Figure 3), possibly due to a higher incidence of habitat fragmentation during environmental changes (Vrba 1980, 1987; Hernández Fernández and Vrba 2005a). Biomes such as the tropical rainforest (I) and the steppe (VII), which lay at opposite ends of the climatic spectrum (warm-humid vs. cold-arid), exhibited a much higher number of specialist species than expected according to null models. This pattern is consistent with the high proportion of specialists found in the Asian steppe and the tropical rainforest of northern South America (Figure 5a). The higher proportion of specialist species observed in tropical rainforest and steppe biomes may partly reflect their extensive spatial extent (Rosenzweig 1995). However, our analyses already accounted for differences in biome area by considering biome carrying capacity in the null models, so the observed excess of specialists cannot be solely attributed to area effects. This suggests that other ecological features, such as climatic stability, play a central role. Two other biomes are present at global climatic extremes: the subtropical desert (III) with high temperature and aridity; and the tundra (IX) which experiences extremely low temperature. However, neither showed more specialist species than expected at the global scale. The total number of squirrel species is very similar in the subtropical desert (13 species) and the tundra (12) biomes, making them the two poorest biomes in terms of squirrel species diversity. On the one hand, their exceptionally low richness might compromise the robustness of the statistical analysis and obscure the assessment of specialist proportion in these biomes compared to null expectations. The prevalence of small sample sizes (low species number) has previously resulted in similar non-significant results for some biomes at the extremes of the global climatic gradient in ruminants at the global scale (Cantalapiedra et al. 2011) and in South American mammals (Moreno Bofarull et al. 2008). On the other hand, this lack of species suggests that subtropical desert and tundra biomes are not adequate for the survival of this group and they are at most marginally occupied, mainly by scant generalist species (Figure 5d–f) whose populations are probably maintained from adjacent biomes.

Interestingly, we did not find higher rates of recent speciation in the regions with the highest species richness, a decoupling also observed in other terrestrial and marine vertebrates (Schluter 2016; Rabosky et al. 2018). Geographic patterns of

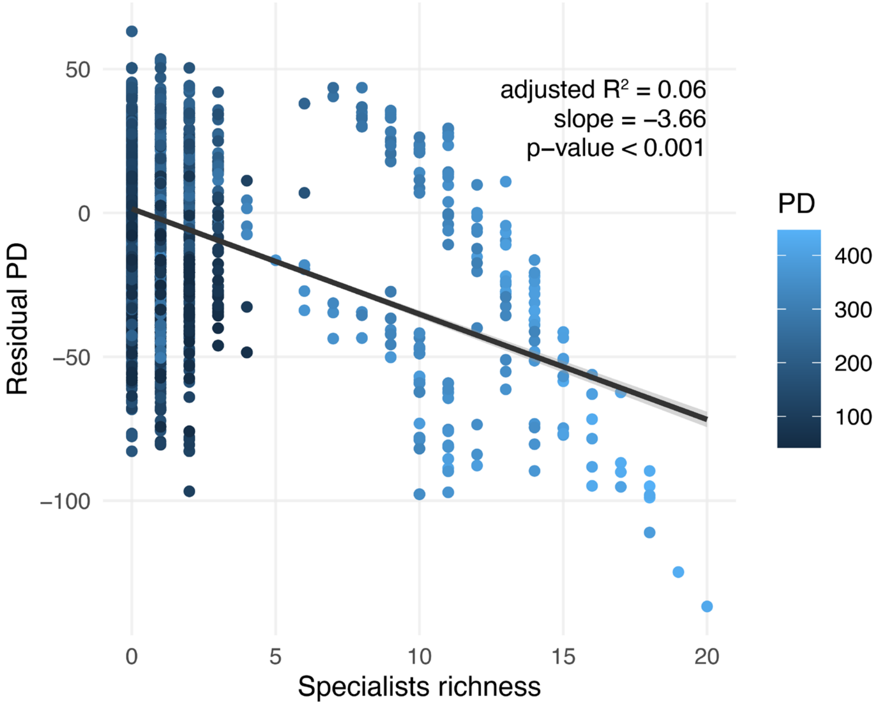

FIGURE 6 | Relationship between specialist richness and richness-corrected phylogenetic diversity (residual PD). Points correspond to cells in the grid map. Colour corresponds to raw phylogenetic diversity values (PD).

high squirrel diversity that we observe today may, therefore, result from past speciation events not recovered by the DR metric, which captures the signal of recent radiation events. Alternatively, current squirrel hotspots may have resulted from the accumulation or immigration of slow-diversifying lineages over long periods of time (Chown and Gaston 2000; Harvey et al. 2020).

Even though squirrels have shown high species-level speciation rates for specialists (Menéndez et al. 2021) and a high number of specialists in Southeast Asia (Figure 5a), we did not find high average speciation rates in this region (Figure 4d), not finding support for our fourth prediction. Instead, we found faster speciation in central Asia and America. This apparent contradiction is consistent with the specialisation and evolutionary history of the squirrel family (Menéndez et al. 2021): specialisation events (and subsequent speciation of specialists) have occurred recently in Holarctic terrestrial squirrels from arid or semiarid environments, while specialisation events in Southeast Asian squirrels are much older (Menéndez et al. 2021). Therefore, recent speciation metrics might reflect accelerated rates resulting from recent specialisation events in northern arid regions. However, these metrics may not capture the accelerated speciation associated with the deep-time specialisation events of Southeast Asian squirrels during the Miocene epoch (Menéndez et al. 2021). In agreement with this, we found that the high recent speciation rates recovered in North America and central Asia are especially clustered in the steppes. The high recent speciation rates in South America may be instead related to the recent colonisation through the Isthmus of Panama < 3 Ma and the later diversification of the *Sciurus* lineage in the Amazonas basin and the Andes (Roth and Mercer 2008; Pečnerová and Martínková 2012).

The ancient specialisation and high speciation of Southeast Asian squirrels could be related to the colonisation of the Sunda Shelf islands such as Borneo, Sumatra, and Java, in the late Miocene, when low sea levels around 10 Ma could have facilitated squirrel dispersal to the islands, and subsequent sea level rising would have isolated these populations triggering speciation (Mercer and Roth 2003; Hawkins et al. 2016). This scenario would explain the decoupling between global geographic patterns for species richness and recent speciation, supporting the idea that patterns of recent speciation rates could be more useful for predicting future richness patterns than for explaining present patterns of biodiversity (Schluter and Pennell 2017; Cantalapiedra et al. 2019). The high phylogenetic diversity found in Borneo, Sumatra and the Malay peninsula (Figure 4b), which hosts a wide representation of phylogenetically distant arboreal and flying squirrels, supports the notion that this vicariance has occurred independently in different lineages, instead of one single colonisation event followed by high intraisland diversification. The latter scenario was most likely the case in other islands such as Sulawesi (Hawkins et al. 2016), which shows low phylogenetic diversity, probably because its location across the Wallace Line beyond the Sunda Shelf made it harder for lineages to colonise (Brodie et al. 2018).

These processes combined to render a diversity and specialists hotspot (Figure 4a and Figure 5a,b) within the Sunda Shelf, particularly in Borneo, where 20 out of 27 species are biome specialists. Some authors have argued that high species richness in the tropics may have resulted from the seasonally stable and favourable climates of these regions, as well as the constancy of the resources, which may promote partitioning of species into finer niches (Dobzhansky 1950; Klopfer 1959; Pianka 1966). In this context, the high heterogeneity of tropical environments in southeast Asia may allow for the coexistence of a high number of specialists compared to the relatively poorer temperate zones. Our results suggest that niche partitioning in the rainforest of southeast Asia, represented by the diversity of biome specialists, might be a determinant factor in shaping patterns of species richness in squirrels. Also, the elevation partitioning could be contributing to high species richness, since in Borneo we find squirrels exclusively adapted to mountains or lowlands (Den Tex et al. 2010; Hawkins et al. 2016).

Overall, squirrel geographic diversity patterns show that important conservation efforts should target the Sunda Shelf (Malay Peninsula, Sumatra, Java, Borneo and associated islands). This region has the highest species richness and greatest phylogenetic diversity for squirrels, and it is a refuge for a significant number of endemic specialist species which are particularly susceptible to extinction pressures associated with climate change events. Furthermore, this region represents a critical biodiversity hotspot not only for the Sciuridae family but also for many other groups (Cardillo and Meijaard 2010; Sodhi et al. 2010; De Bruyn et al. 2014).

Author Contributions

I.M., A.R.G.C., and M.H.F. conceived the study. I.M. compiled the data and led the analyses, with methodological and conceptual input from M.H.F., J.L.C., J.S.P., A.R.G.C., S.G. and F.B. I.M., A.R.G.C. and M.H.F. contributed to interpretation of results and discussion of biogeographic and evolutionary implications. I.M. did the figures, with inputs from M.H.F., J.L.C., J.S.P., A.R.G.C., S.G. and F.B., E.G., Á.Q. and M.Á.Á.-S. I.M. led the writing of the manuscript, with inputs from M.H.F., A.R.G.C., J.L.C., S.G., F.B., E.G., Á.Q. and M.Á.Á.-S. All authors contributed to revisions and approved the final version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used in this study are provided in the Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Code S1.** R script used to generate global geographic patterns of squirrel diversity and specialisation. The code calculates grid-cell species richness, specialist, generalist and extreme generalist richness, Faith's phylogenetic diversity, richness-corrected phylogenetic diversity (residual PD) and mean recent speciation rates (DR statistic) using equal-area hexagonal grids of 50 × 50 km resolution. **Data S1:** Species-level dataset of extant squirrels (Sciuridae) including biome occupancy, biome specialisation index (BSI), specialisation category (specialist, moderate generalist, extreme generalist), taxonomic affiliation and indication of species incorporated without molecular data using the TACT method. **Data S2:** Set of 100 time-calibrated phylogenetic trees of extant squirrels (Sciuridae) used to estimate recent speciation rates (DR statistic). Trees are based on a molecular backbone phylogeny and include additional species without molecular data incorporated at the genus level using the taxonomy-based TACT approach. **Table S1:** Observed and expected proportions of biome specialisation categories (specialists, moderate generalists and extreme generalists) across the family Sciuridae and major subfamilies with more than 10 species. Expected values were obtained from 10,000 MCMC randomizations of the biome presence–absence matrix, constraining biome species richness. Statistical significance indicates departures from random expectations. **Table S2:** Observed and expected percentages of specialist squirrel species (BSI = 1) across global biomes. Expected values were derived from 10,000 MCMC simulations of the biome presence–absence matrix, maintaining biome-specific species richness. Statistical significance indicates departures from random expectations.