

Scale dependence of avian functional rarity reveals mismatches between global and local conservation priorities

Authors

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Abstract

Aim. Spatial scale shapes both how rarity is defined and how conservation priorities are derived from it, yet most functional rarity assessments rely on a single (often global) reference pool. We test how the scale dependence of functional rarity affects hotspot identification and the alignment of global versus local conservation priorities in birds.

Location. Global.

Time period. Contemporary.

Major taxa studied. Birds (10,906 species).

Methods. Using AVONET morphological traits and global distributions, we quantified functional rarity as the average of two components: trait distinctiveness (mean distance to other species in trait space) and geographic restrictedness ($1 - \text{occupancy}$). We computed both components at four nested spatial scales (global, biogeographic realm, biome-within-realm, and local assemblage context). We then mapped assemblage-level functional rarity-weighted richness (Frwr) on a $\sim 100 \times 100$ km grid, defined hotspots under two policy-relevant thresholds (top 7.1% and top 30% of cells), and quantified hotspot congruence among scales.

Results. Trait distinctiveness was nearly invariant from global to biome scales, whereas restrictedness strongly decreased at finer scales, driving marked scale dependence in functional rarity. Hotspots identified using Frwr showed very low spatial overlap across scales ($<4\%$ shared), indicating that globally derived priorities often miss assemblages that are functionally rare in regional or local contexts. Multiscale hotspot convergence was concentrated in a limited set of regions, including major tropical mountain systems and island arcs.

Main conclusions. Functional rarity offers a trait-based perspective on conservation value, but its interpretation depends on the reference pool and thus on scale. Integrating multiple scales is necessary to reconcile global biodiversity targets with the protection of regionally and locally distinctive ecological strategies.

Keywords

functional rarity; scale dependence; conservation biogeography; birds; spatial prioritization; morphological diversity; functional distinctiveness; restrictedness

Introduction

Rarity is a pivotal concept in conservation biology, community ecology, and biogeography (Enquist et al., 2019; Gaston, 1994; Lovejoy et al., 1986; Rabinowitz, 1981). Conservation biology generally focuses on geographically restricted and scarce species given that they are more vulnerable to extinction, and on biogeographic regions that accumulate such species (Rodrigues et al., 2006). Another important approach in conservation lies in identifying which species' attributes lead to rarity (Gaston & Blackburn, 1996; Murray et al., 2002), and how extinction of rare species could affect ecosystem functioning (Dee et al., 2019; Jain et al., 2014). The underlying idea is that rare species might have particular traits that are linked to their rarity, and/or perform important and unique functions in ecosystems (Leitão et al., 2016; Mouillot et al., 2013). These considerations have led to the development of functional trait rarity (hereafter functional rarity) (Violle et al., 2017) which jointly considers species geographic restrictedness (i.e., species occupying larger or smaller areas) and trait distinctiveness (i.e., species that are closer or further from other species in trait space). To date, a few studies have shown how functional rarity was distributed across the globe and across taxonomic groups, and have described areas of potential primary importance for conservation given the number of functionally rare species found in a given area (Auber et al., 2022; Grenié et al., 2018; Loiseau et al., 2020; Trindade-Santos et al., 2022). One of the main justifications for highlighting hotspots of functionally rare species is that areas sheltering many species with rare traits enclose functions, forms, and strategies which are particularly vulnerable (Auber et al. 2022, Hughes et al. 2022) and might have a unique role in ecosystem processes and stability (Delalandre et al., 2022; Sosiak & Barden, 2021). Because species geographic restrictedness and trait distinctiveness are not expected to correlate (Grenié et al., 2018; Loiseau et al., 2020), regions that accumulate geographically restricted species, like endemic species on islands (Kier et al., 2009), might differ from the regions that accumulate species with distinct traits (Loiseau et al., 2020). So, redefining rarity in terms of both geographic restrictedness and trait distinctiveness may provide a more integrative assessment of conservation priorities (Kondratyeva et al., 2019; Violle et al., 2017).

Most functional biogeography studies have considered functional rarity from a global perspective (Rodrigues, 2025), by computing species restrictedness on their global extent of occurrence (range size across Earth), and their trait distinctiveness relative to the global species pool (all species on Earth) (Grenié et al., 2018; Loiseau et al., 2020). Although computing species distinctiveness relative to the global species pool is relevant in most cases, focusing on smaller scales provides a more functionally-oriented perspective of trait-based conservation with species potentially having unique traits in a given region, but not globally (Gaüzère et al., 2023). In this case, the functions played by these species are unlikely to be replaced if they become regionally extinct and can be considered regional conservation priorities, but not global. In line with recent calls for integrating knowledge across scales in conservation (Chaplin-Kramer et al., 2022; Rodrigues, 2025), we argue that considering multiple scales when performing functional rarity assessments improves its relevance for conservation biogeography (Hughes et al., 2022). First, analysing scale-dependence of geographical restrictedness vs scale-dependence of trait distinctiveness might provide useful insights to understand when scale matters the most for these two facets of species rarity. Second, identifying when the scale of study is not aligned with the conservation aspect under scrutiny can prevent spurious use of the concept (Gaüzère et al., 2023; Wyborn & Evans, 2021). Although "scale" can have various definitions across ecology and biogeography, it generally corresponds to hierarchical levels allowing us to navigate between spatial extents, eco-evolutionary processes and socio-environmental contexts (Figure 1). Conservation actions depend on the ecological processes targeted for preservation, the political boundaries within which conservation is conducted (as policies are implemented at continental, national, or sub-national scales), and the area related to conservation decisions (Hartley & Kunin, 2003). This is essential to consider, as species can have starkly different occupancy and threat status depending on the scale considered. For example, the corn crake (*Crex crex* L.) - a bird species largely distributed across the globe- is considered least concern at global scale (BirdLife International, n.d.), but considered as endangered in France (INPN, n.d.) where it is the focus of European and National conservation programs. The corn crake exemplifies how scale and context can be important when

examining rarity in conservation. Furthermore, asking the question “why should we conserve rare species and functions?” brings us back to considering the scale at which the conservation interest is expressed. For example, the functional distinctiveness of a species at global scale brings strong conservation interest because a form or function is unique at global scale and as such has a particular value (Echeverri et al., 2020). Accordingly, birds with extreme morphological trait values (e.g., lack of wings, long beak, large body, see Appendix 1 - Trait distribution and correlations) would represent unique sets of traits worldwide (i.e., functionally distinct species at the global scale) that can be considered of conservation interest for the sake of nature (Díaz et al., 2018). Just as Evolutionarily Distinct and Globally Endangered (EDGE) species are of important conservation interest because their extinction represents a loss of unique evolutionary history and biodiversity (Isaac et al., 2007), global extinction of functionally distinct species would represent a disproportionate loss of phenotypic diversity. Otherwise, conserving functionally distinct species at local scales is important because it is at the local scale that functional traits are expressed and contribute the most to ecosystem functioning and stability (Delalandre et al., 2022).

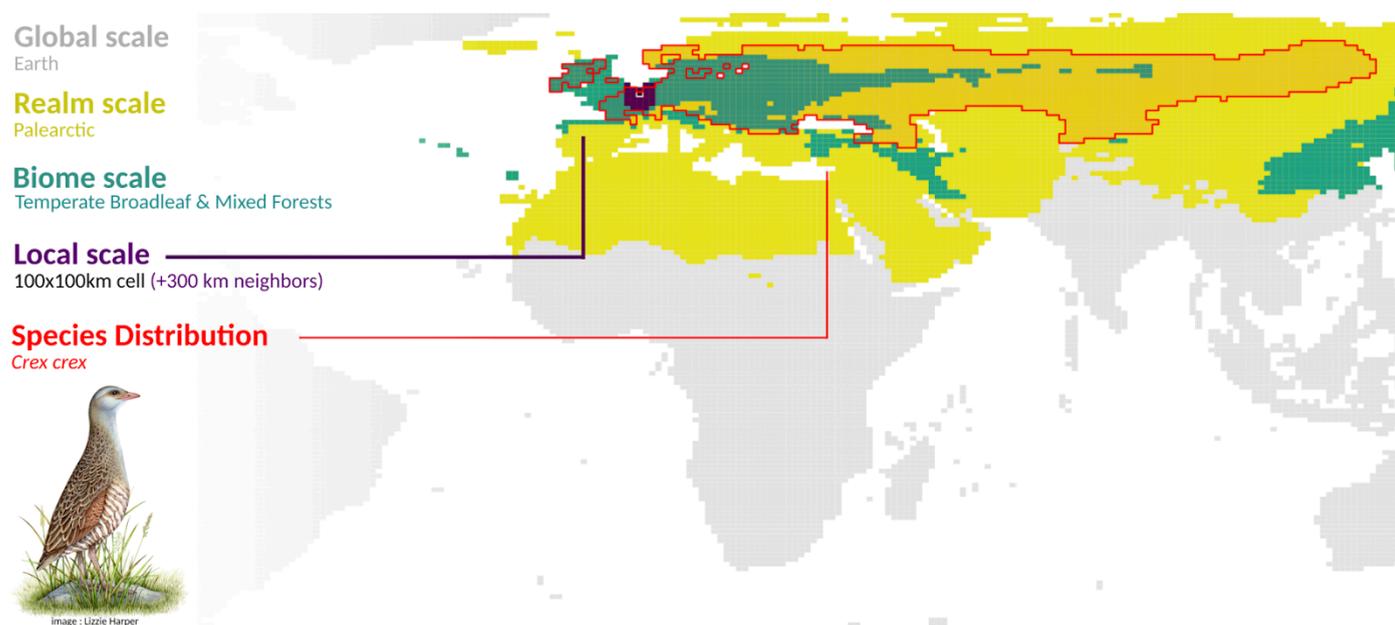


Figure 1. The biologically relevant scales considered in this study are the global scale (world, cropped, in grey), the realm at which geographic barriers and evolutionary history play the major role (in yellow, here the Palearctic), the biome scale at which climate is the predominant factor (in green), and the local scale at which local abiotic factors and biotic interactions are conjointly shaping species assemblages (here the cell in red or the neighbors cells within a 300km distance in purple - see Methods).

A large body of macroecological theory predicts that many biodiversity attributes should scale predictably with spatial grain and extent. In particular, geographic range size distributions are strongly right-skewed, implying that most species appear rare at broad extents but increasingly common at finer scales (Gaston, 1994; Rahbek, 2004). Similarly, trait space occupation and trait–abundance relationships are known to scale with species richness, environmental filtering, and evolutionary history (Munoz et al., 2023a; Pigot et al., 2020). As a consequence, some scale-dependent patterns in rarity are expected *a priori* and can be interpreted as null expectations rather than novel phenomena. What remains poorly understood is how these well-known scaling relationships propagate into functional rarity and, critically, how they reshape spatial conservation priorities across scales.

To demonstrate the need for considering the scale at which functional rarity is computed when providing inference of species or area values for conservation purpose, we here explore global patterns of birds’ species and assemblage functional rarity across scales. We focus on birds because they have often been considered as prime features for conservation actions (along with mammals and habitats), and they are one of the most studied taxonomic groups for which traits and geographic distribution are well described and available (Tobias et al., 2022). We considered a set of morphological traits directly linked to species niches, functions, and

eco-evolutionary processes (Pigot et al., 2020). By combining distribution ranges and morphological traits of most birds in the world, we developed a workflow to compute each bird species' functional rarity at global, realm, biome and local scale. We first focused on species level to show whether and how scale of computation can affect species (functional) rarity metrics. We then calculated assemblage levels aggregated metrics (within ~100 x 100 km grid cell), in particular functional rarity weighted richness - a metric combining species complementarity, diversity, and ecological originality to assess hotspots distribution across spatial scales. By assessing species' functional rarity with a multi-scale perspective, our study unveils hotspots often overlooked by conventional global approaches, underscoring the pressing need to integrate both functional traits and scale-dependence into conservation planning.

Methods

Data

Traits | We used the AVONET database, a comprehensive dataset on the morphological traits and geographic distributions of 11,009 bird species representing >99% of the total number of described species (Tobias et al., 2022). We used a set of 11 morphological traits describing the phenotype of birds: beak length measured from tip to skull along the culmen; beak length measured from the tip to the anterior edge of the nares; beak depth; beak width, tarsus length; wing length from carpal joint to wingtip measured on the unflattened wing; secondary length from carpal joint to tip of the outermost secondary; Kipp's distance, measured directly or calculated as wing length minus first-secondary length; tail length, hand-wing index, and body mass. When taken together, these eleven traits describe many aspects of birds' phenotype, and have been previously related to (i) the response of species to their environment (response traits), (ii) the functions performed by the species in the ecosystem (effect traits), and (iii) eco-evolutionary processes such as evolutionary adaptation (Pigot et al., 2018, 2020). Importantly for a multi-scale analysis, morphological traits exhibit strong phylogenetic structure and scale predictably with environmental gradients, making them particularly suited for cross-realm and cross-biome comparisons. Although some morphological traits showed pairwise correlations exceeding 0.75 (see Appendix 1 - Trait distribution and correlations), we retained the full trait set to preserve a comprehensive view of avian morphology. This ensures that both size-related and shape-related dimensions are represented, avoiding undue emphasis on any single functional axis. All traits were log-10 transformed and scaled for analyses (see Appendix 1 - Trait distribution and correlations).

We acknowledge that other widely used trait databases capture complementary aspects of avian ecology, such as diet and foraging strata (EltonTraits) or nest characteristics (Chia et al., 2023; Sheard et al., 2024). However, these traits are often categorical, context-dependent, or sparsely documented across regions, which complicates their integration into scale-explicit rarity metrics. Our objective here was not to exhaustively represent all functional dimensions, but to assess how a consistent and evolutionarily grounded trait space behaves across spatial scales.

Species assemblages | Local bird assemblages were defined using species distribution range data provided within the AVONET dataset (Tobias et al. 2022), which includes native and resident or breeding ranges pre-mapped onto a uniform global grid of approximately 100 km x 100 km cells in the Behrmann equal-area projection (ESRI:54017). While relatively coarse for defining a "local" scale (see below), this resolution has been shown to reduce commission errors (i.e., false presences) in large-scale distribution data (Belmaker & Jetz, 2011; Hurlbert & Jetz, 2007). From the 11137 species for which we had the distribution ranges, we removed 48 species for which distribution ranges appeared erroneous following visual inspection, and 183 species for which trait data were not available, resulting in a final dataset of 10,906 species. We chose not to implement trait imputation for the small fraction of excluded species (<2%), as imputation uncertainty may disproportionately affect estimates of trait distinctiveness, which directly relies on interspecific distances in trait space (Penone et al., 2014).

Scales

We focused our study on four different spatial scales: global, realm, biome, local (Figure 1).

We defined the **global scale** as the entire terrestrial land of the world where birds are found. The unit-scale is the total terrestrial land mass, of ~ 150 million km² area. We focused on terrestrial land and omitted oceans for which range data are not sufficiently reliable (Hurlbert & Jetz, 2007).

We defined the **realm scale** as the 9 biogeographic realms following WWF (Olson et al., 2001). The unit-scale is a realm, the area can vary between realms (from 1 million km² to 54 million km²).

We defined the **biome scale** as the WWF biomes (Olson et al., 2001) intersected with biogeographic realms, because the same biome can be found in several realms. For example, there are Taiga biomes in both the Nearctic and the Palearctic realms. Our biome scales consider them as two separate entities. Considering biomes within realms, we obtained 66 entities (see Appendix 2 - List of biomes and realms combinations). The unit-scale is a biome within a realm. These entities can have vastly different areas (min 18619km², max 30200476 km², mean 5307499km²).

The **local scale** is defined as a cell. The unit scale is the area of a cell, i.e. ~10000 km² (100km x 100km).

Species rarity metrics

For each species in the dataset, we separately computed the two components of functional rarity, namely the **(geographical) restrictedness** and the **(trait) distinctiveness** at each scale (Violle et al., 2017).

The **restrictedness (Re)** of a species is calculated as $1 - \text{species area occupancy}$, where the area occupancy is defined as $\text{species presence area} / \text{total area}$ of the unit-scale considered (Figure 1). At the local scale, we only know the presence-absence of species at the cell resolution. Hence, we defined the local area occupancy as the number of cells in which the species is present within a distance of 300km of the focal cell divided by the total number of cells existing within the same distance. We chose 300 km as a compromise between (i) including enough neighboring cells to obtain stable occupancy estimates per species, (ii) maintaining spatial coherence of regional pools, and (iii) remaining within typical dispersal and biogeographic structuring distances for birds. This choice emphasizes local-to-regional context rather than continent-wide pools. We note that different radii may shift absolute Re values but not the qualitative scale-dependence we report

The trait **distinctiveness (Di)** of a species is calculated as the mean distance between the focal species and all other species present within the unit-scale considered (global, realm, biome, or local, see Figure 1), based on Euclidean distance of the transformed trait values. We used the `distinctiveness_com()` function of the *funrar* R package (Grenié et al., 2017).

For each species found within a cell, we computed its restrictedness and its trait distinctiveness for the corresponding local, biome, realm, and global scale.

The **functional rarity (Frar)** of a species was calculated as $f_{di}(Di) + f_{re}(Re) / 2$, where $f_{di}()$ and $f_{re}()$ are transform functions that normalize the highly skewed distributions of Di and Re. $f_{di}()$ transforms the Di values to emphasize smaller values by applying a square root transformation while normalizing to a range of 0-1. $f_{re}()$ transforms Re to give greater range to lowest values, and smaller for values closer to 1, while normalizing to a range of 0-1. These monotonic transformations preserve species ranks, while improving Frar distributional symmetry and comparability across scales. Visualization of transformation and their effect on Frar values are available in Appendix 3 - Transformations.

Cell assemblage rarity metrics

Distribution moments. Within each cell, we computed the arithmetic mean and variance of the distribution of restrictedness, distinctiveness and functional rarity computed at each scale. We filtered out cells with less than ten species (representing 5.2% of the total cells) that occur in harsh or isolated environments (polar/desert islands) to avoid extreme values due to the low number of species.

Functional rarity weighted richness. We proposed Functional rarity weighted richness (Frwr), that summarizes the cumulative contribution of functionally rare species within assemblages. Conceptually, Frwr is inspired by rarity-weighted richness approaches developed for conservation prioritization (Albuquerque & Beier, 2015; Williams et al., 1996). Here, we extend this logic to functional rarity, using Frwr as a transparent and policy-relevant heuristic rather than an attempt to decouple rarity from richness entirely. Within each cell, we computed **Frwr** at each scale, as follows:

$$Frwr = \sum_{i=1}^n w_i$$

Where W_i is the weight of each species based on its Functional rarity at a given scale. For each species at each scale, W_i was calculated as $Frar^{10}$ in order to put a large weight on species with highest Frar values, and normalized between 0 and 1 in each scale-unit. As a summed index, Frwr is expected to covary with species richness, and is used here to capture differences in functional composition among assemblages with comparable richness (Appendix 4 - relation between Frwr and species richness).

Defining hotspots of functional rarity across scales

We used **Functional rarity weighted richness** to rank the cells from the highest to the lowest values. We defined two thresholds for defining hotspots. The first threshold to define hotspots was set to top 7.1% of cells ($n = 1224$) because it provided a cumulative area equivalent to the area protected globally (WDPA equivalent), generally considered as cells with more than 17% of their area covered by the protected area IUCN categories 'Ia - strict nature reserve', 'Ib - wilderness area' or 'II - national park' (Pollock et al., 2017). The second threshold was set to the 30% cells because it provided an equivalent to the "Kunming-Montreal Global Biodiversity Framework" (GBF) committed to protect at least 30% of both land and sea before 2030. We relied on functional rarity weighted richness to define hotspots because it provides a link between hotspot identification and conservation planning based on functional rarity, as functional rarity weighted richness is the trait-based equivalent of the rarity weighted mean, which has been identified as a simple and efficient solution for conservation planning that aims to maximize local diversity (Pollock et al., 2017), and provides outputs which are close to solutions based on more complex algorithms defining a minimum set of complementary sites that maximize species coverage within the reserve network (Albuquerque & Beier, 2015), see also <https://rpubs.com/jlehtoma/priocomp>.

To compute the total area protected globally, we used the World Database on Protected Areas (WDPA). We only considered the most restricted IUCN categories (Categories 'Ia - strict nature reserve', 'Ib - wilderness area' and 'II - national park') since these categories protect threatened species more effectively (Loiseau et al., 2021). The calculation was processed using the "Tabulate intersection" function in ArcMap.

Results

Species Functional trait rarity across scales

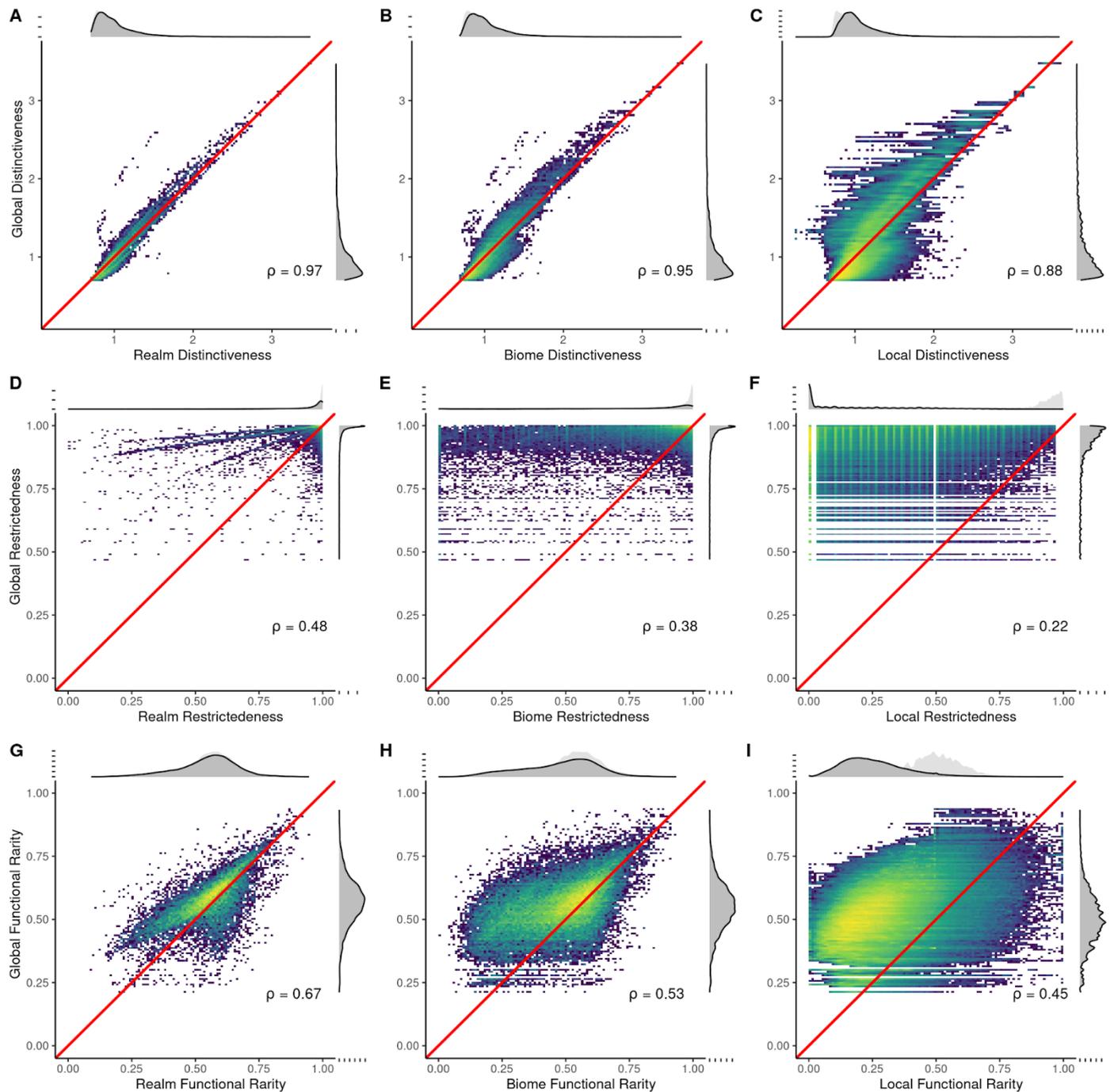


Figure 2. Variation of Species rarity metrics between Global scale and Realm (left), Biomes (center) and Local (right) scales for: species distinctiveness (top, A-C), species restrictedness (middle D-F), and species functional rarity (bottom G-I). Surface color shows the density of species (differing between each panel), from low density (blue) to high density (yellow). Red line shows the 1:1 relationship. Marginal density plots show the density distribution of values along each axis, with light grey distribution in the background showing global scale distributions as a reference. ρ (bottom right of each panel) is Spearman's rank correlation coefficient associated with each relationship.

Trait distinctiveness (Figure 2, A-C) remained relatively stable across scales, with high correlations between global and realm ($\rho=0.97$) or biome ($\rho=0.95$) scales. At local scale, the trait distinctiveness tended to

deviate more from global scale values ($\rho = 0.88$, Figure 2C). When projected into the bird's morphospace, we found that large-bodied, winged species were more distinct at global than local scale, while small-winged species were generally more distinct at local than global scale (see Appendix 5 - Variation of distinctiveness mapped into morphological space). For instance, large sea birds such as *Diomedea epomophora* that were distinct at global scale were less distinct within their realm and biomes, within which they represent most of the bird species. On the contrary, the South Georgia pipit (*Anthus antarcticus*) was more distinct within its realm or biome than globally.

In contrast, restrictedness (Figure 2, D-F) showed a stronger scale dependence, with rank-based correlations dropping significantly from global to realm ($\rho = 0.48$), biome ($\rho = 0.38$) and local scales ($\rho = 0.22$). The marginal distributions reveal a clear shift towards lower restrictedness values at finer scales, indicating that species tend to become less geographically restricted as the scale narrows.

Functional rarity showed significant scale-dependent patterns, with decreasing congruence between global rarity values and those at finer spatial scales (Figure 2, G-I). At the realm scale (Figure 2G), the relatively high ($\rho = 0.66$) indicates a moderate correlation, suggesting that global rarity patterns varied with those observed at the realm level. As spatial scale narrows to biome (Figure 2H) and local (Figure 2I) levels, the ρ values decrease ($\rho = 0.53$ and $\rho = 0.45$, respectively), and points deviate more widely from the 1:1 line, suggesting a decoupling between global and local scales with a substantial decrease of functional rarity, as shown by marginal density plot in Figure 2.I.

Cell-averaged Functional trait rarity is not consistent across scales

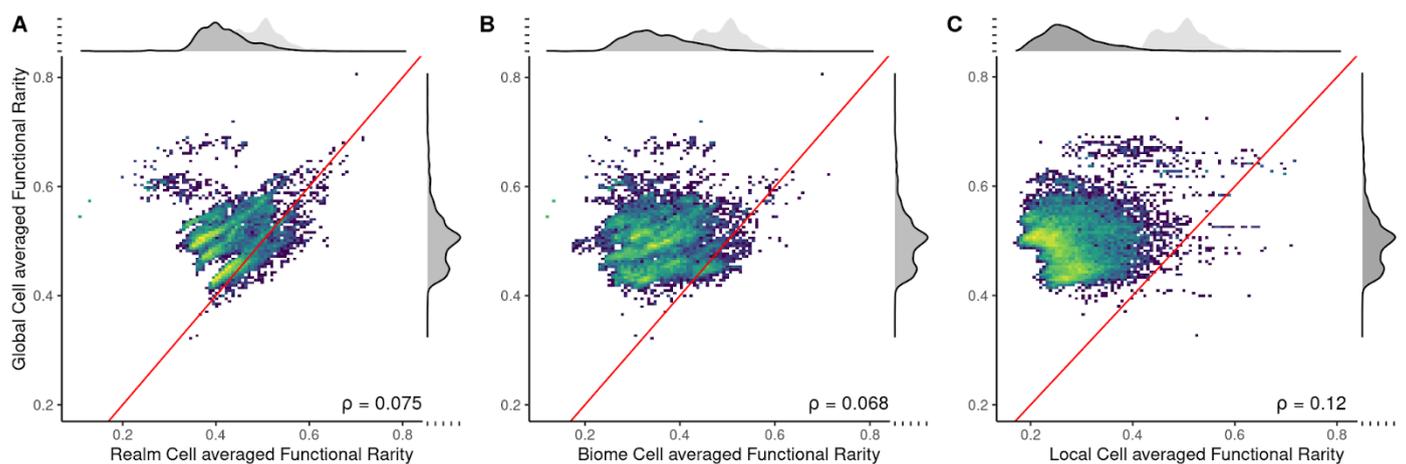


Figure 3. Variation of cell-averaged Functional rarity between scales : Global vs. Realms (A), vs. Biomes (B) and vs. Local scales (C). Surface color shows the density of cells, from low density (blue) to high density (yellow). Red line shows the 1:1 relationship. Along each axis, marginal density plots show the density distribution of values in dark grey, with the global scale density added in light grey on the x-axis to ease comparison. ρ (bottom right of each panel) is Spearman's rank correlation coefficient associated with each relationship.

Comparing the cell-averaged Functional rarity (i.e., mean value of the species present in a given cell) reveals the weak correlation between cell-averaged functional rarity across global, realm, biome, and local scales (Figure 3), as shown by the very low ρ values : 0.075 for realm (Figure 3A), 0.068 for biome (Figure 3B), and 0.12 for local (Figure 3C). These results indicate that global functional rarity patterns are largely decoupled from those observed at finer spatial scales. The marginal distributions reveal that the range of functional rarity is relatively consistent across scales, but the mean of the distribution shifts toward lower values of rarity with decreasing scale. This shows that —although the species present in each grid cell stay exactly the same— changes in species rarity score due to different scales of computation leads to important variations in cell-averaged functional rarity. These findings highlight that functional rarity, when averaged at the cell level, is highly sensitive to the spatial scale of analysis, emphasizing the importance of scale when interpreting patterns of diversity.

Distribution of functional rarity hotspots: differences and congruences between scales

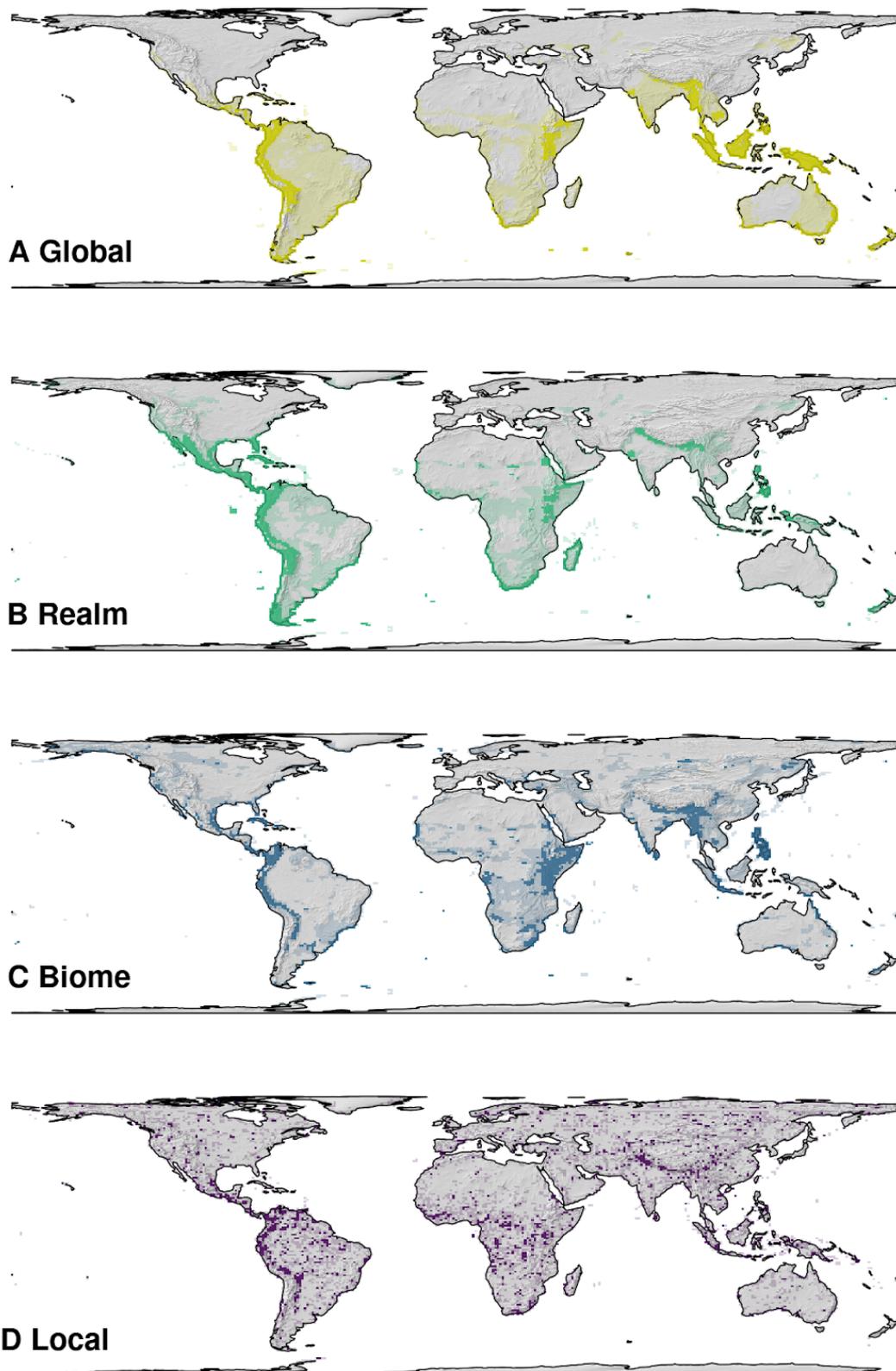


Figure 4. Global distribution of functional rarity weighted richness (Frwr) across four spatial scales of computation. Maps display hotspots of functional rarity weighted richness calculated at: (top to bottom) global, realm, biome, and local scales. Color transparency reflects the threshold for consideration of hotspots, with opaque-colored cells corresponding to the current WDPA equivalent (top 7%), and semi-transparent cells corresponding to the global biodiversity framework equivalent (top 30%).

The spatial distribution of the functional rarity weighted richness showed distinct patterns emerging across the global, realm, biome, and local scales.

When based on **global scale** metrics (Figure 4A, yellow), core hotspots (opaque cells, 7% top cells “WDPA equivalent”) are mainly found in three well-known centres of endemism: the Tropical Andes (stretching from Venezuela to central Bolivia), the Sundaland–Wallacea–New Guinea archipelagos and the adjoining northern fringe of Australia, and in East Africa (Eastern Afromontane). Secondary hotspots (semi-transparent, 30% cells, “GBF equivalent”) expand these areas into the Amazon forelands, the Himalayan foothills and south-eastern Africa, but leave most temperate zones devoid of global-scale rarity.

When based on **realm scale** metrics (Figure 4B, green), the pattern fragments and new centres of functional rarity hotspots appear. The Tropical Andes remain prominent, but core hotspots expanded in Mesoamerica and the Caribbean, the Chile-Patagonian temperate forests, the Eastern Afromontane–Cape Floristic axis, and Madagascar, while other global scale core hotspots such as the Sundaland–Wallacea–New Guinea archipelagos and Australia disappear. Secondary hotspots did not substantially change, apart from expansion in North America

When based on **biome scale** (Figure 4C, blue), core hotspots become more tightly linked to specific climatic or vegetation types, aligning with unique ecological characteristics defined by specific biome boundaries. In South America distribution of hotspots shrinks onto the páramo and montane forests of the Central Andes; in Africa hotspots expand in the Horn of Africa and East African savannas; in Asia hotspots appear in the Western Ghats, Sri Lanka, Eastern Himalaya and Indochinese subtropical forests, while insular hotspots are more identifiable over the Philippines. Many continental lowlands that were identified as secondary hotspots at broader scales disappear, and are replaced by scattered areas in temperate areas. .

When based on **local scale** (Figure 4D, purple), functional rarity hotspots show a mosaic map in which core cells punctuate virtually every tropical mountain chain and island arc. Denser distributions are found in the central Andean cordillera, Southern Africa, Himalaya, and Indonesia. Secondary hotspots show low spatial aggregation and are distributed all across the globe.

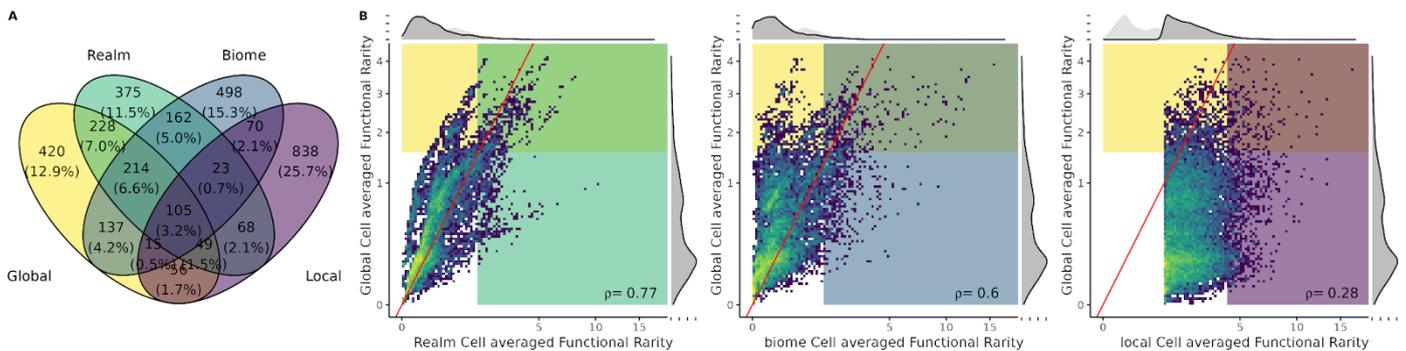


Figure 5. Congruence of functional rarity hotspots across scales. (A) Venn diagram showing overlap among hotspot cells (top 7.1% Frwr) identified at global, realm, biome, and local scales. (B–D) Relationships between cell-averaged functional rarity computed at the global scale and at the realm, biome, and local scales, with Spearman's rank correlation ρ . Background colors shows overlap of hotspots corresponding to panel A.

The Venn diagram (Figure 5A, left) quantifies overlap of functional rarity hotspots across spatial scales, with most hotspots being unique to a scale. Only 105 (3.2%) hotspots are shared across all four scales, indicating weak overlap between scales. These critical hotspots across multiple spatial scales are concentrated in a few key regions globally (purple and blue cells on the map Figure 6):

In the tropical Andes, where a continuous multiscale hotspot (in purple) belt stretches from the Cordillera de Mérida (Venezuela) through the Colombian and Ecuadorian cordilleras into northern Peru. In the Eastern Afromontane, where multiscale hotspots appeared in the Ethiopian Plateau and the string of mountains that

run south through Kenya and Tanzania's Eastern Arc. Along the Eastern Himalaya and into the Sino-Burmese highlands (Myanmar). Specifically, 420 (12.9%) hotspots are exclusive to the global scale, while 838 (25.7%) are exclusive to the local scale. Hotspots shared between realm and biome levels account for 162 (5%) of the total. The geographic distribution of these hotspots (Figure 5B) further highlights this disparity, with many regions only prioritized at only one scale.

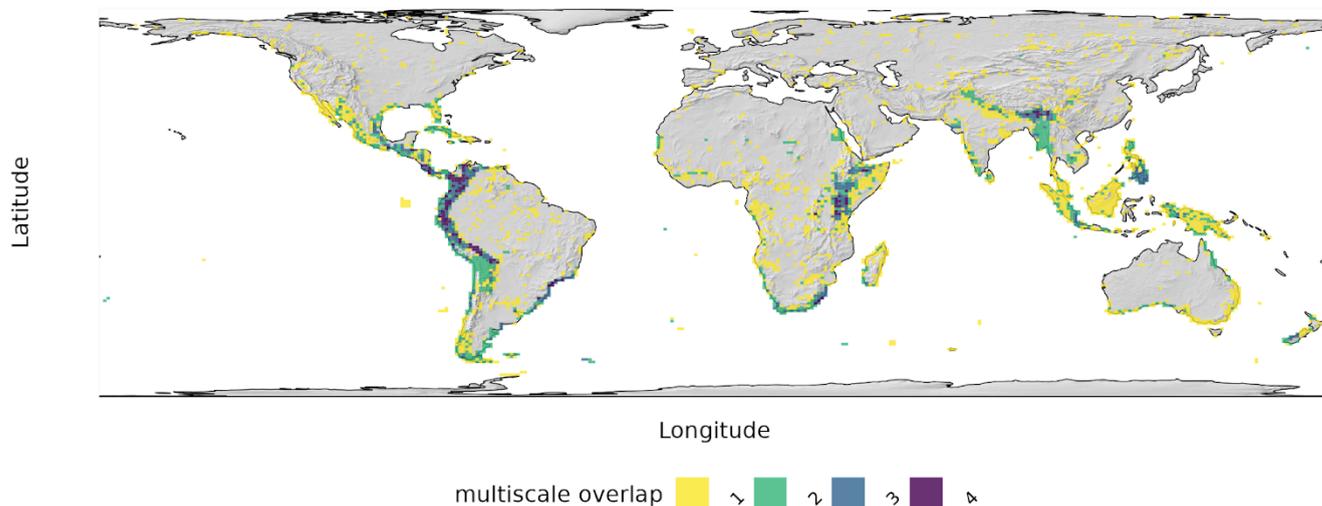


Figure 6. Spatial distribution of core functional rarity hotspots according to the number of spatial scales at which each cell is identified as a hotspot. Values indicate the count of scales (from 1 to 4) for which a given cell ranks within the top 7% of *Frwr* values. Darker colors indicate convergence of conservation priority across multiple scales, without specifying which scale combinations are involved.

Discussion

Our analysis of global avian trait biodiversity highlighted scale dependence in species functional rarity, although these were driven by the scale dependence of species' geographic restrictedness rather than species distinctiveness. These variations substantially influenced spatial patterns of trait rarity and the identification of biodiversity hotspots of functional rarity. Several patterns reported here—such as the strong scale dependence of geographic restrictedness and the right-skewed distribution of rarity—are consistent with long-standing macroecological expectations. Rather than challenging these expectations, our results clarify how they propagate into functional rarity and, in turn, reshape spatial conservation priorities in ways that are rarely made explicit. Understanding these scale-dependent dynamics is therefore less about documenting unexpected patterns than about improving how rarity-based indicators are interpreted and used in conservation decision-making. Just as with spatial planning based on species distributions, setting local targets for trait conservation may be a useful complement to global or regional decisions. Although species with particular traits need to be conserved at the local scale to conserve the function they hold, they also need to be present and remain distinct in the surroundings to ensure their persistence in the long-term (Mouillot et al., 2014). This tension between local functional expression and broader-scale persistence lies at the core of scale-dependent conservation planning (Hartley & Kunin, 2003).

Our analyses revealed that trait distinctiveness was stationary across scales, with species rankings being largely conserved from the global to the realm and biome levels. This near scale-invariance suggests that trait distinctiveness provides a robust and consistent measure of species' ecological originality. This pattern is consistent with recent work showing that trait distinctiveness is weakly or inconsistently related to geographic range size, particularly among range-restricted species, while becoming more strongly associated

with range size among widespread taxa (Affleck & McGeoch, 2024). Our results therefore do not contradict previous findings on the relationship between trait distinctiveness and range size, but extend them by demonstrating that this decoupling persists across multiple spatial scales and has direct consequences for conservation prioritization. As such, distinctiveness may provide a reliable basis for broad-scale, trait-based species triage in conservation planning. At the local scale, we observed greater deviations, consistent with previous studies at the community level (Gaüzère et al., 2023; Kondratyeva et al., 2020), and indicative of the growing influence of environmental filtering in promoting local coexistence of species with analogous traits (Munoz et al., 2023b). Examples such as large-bodied seabirds (such as the Southern Royal Albatross, *Diomedea epomophora*) losing relative distinctiveness locally, or narrowly specialized species (e.g., the South Georgia pipit, *Anthus antarcticus*) becoming more distinctive within regional contexts, illustrate that distinctiveness is primarily a global attribute that can nonetheless be modulated by the composition of local and regional species pools. Importantly, although functional rarity tends to decrease locally, this does not diminish their conservation relevance: local-scale rarity reflects unique trait combinations expressed under local filters, which are directly linked to ecosystem functioning and resilience (Delalandre et al., 2022).

While our analyses centered on distinctiveness, the related metric of trait uniqueness—the distance to the nearest functional neighbor—would provide a complementary view of functional rarity at any scale. Distinctiveness highlights overall isolation and is robust to richness variation, whereas uniqueness is more sensitive to functional insurance among closely related trait profiles. Investigating uniqueness varies across scales would further help identify assemblages where the loss of a single species could most compromise functional integrity, a key consideration for conservation planning.

In contrast to distinctiveness, geographic restrictedness exhibited strong scale dependence, with species appearing increasingly widespread as the spatial extent narrowed. This pattern reflects a well-established macroecological property of range-size distributions and should be interpreted as a baseline scaling property rather than a novel empirical finding per se (Gaston, 1994; Rahbek, 2004). It emphasizes, however, that restrictedness is inherently contextual. The contribution of our analysis is not to demonstrate this scaling, but to show how it dominates functional rarity estimates and drives the observed decoupling between global and finer-scale rarity patterns. From a conservation perspective, this implies that restrictedness assessed at regional or local scales captures the position of populations relative to their overall distribution, rather than global rarity per se. Such information is essential for identifying peripheral, isolated, or range-margin populations that may harbor unique genetic or functional variation (Eckert et al., 2008), even in otherwise widespread species.

Together, these results highlight the decoupled but interacting behavior of distinctiveness and restrictedness across scales: restrictedness requires careful spatial contextualization, whereas distinctiveness is comparatively robust to scale choice. This contrast has direct implications for conservation prioritization. Focusing on functionally distinct species may represent a strategic advantage, as it reduces sensitivity to scale mismatch while capturing both ecological and evolutionary dimensions of biodiversity. At local scales, such species contribute disproportionately to ecosystem functioning and stability (Delalandre et al., 2022), whereas at global scales they represent irreplaceable components of phenotypic diversity and long-term adaptive potential (Affleck & McGeoch, 2024; Loreau et al., 2003). This dual role strengthens the case for integrating trait-based metrics into conservation frameworks (Pavoine & Ricotta, 2024; Rodrigues, 2025), not as substitutes for taxonomic or threat-based criteria, but as complementary dimensions that are less prone to scale-related misalignment.

At the assemblage level, averaging species functional rarity within cells revealed weak congruence across scales, underscoring a decoupling between global-scale and finer-scale spatial patterns. Because local assemblages often comprise habitat-filtered sets of species with convergent traits, local functional rarity can be low even in areas of high species richness or endemism. This reinforces the need for scale-aware interpretation: identical species compositions can yield contrasting rarity values depending on the reference pool. From an applied perspective, this supports a two-tier strategy, in which realm- or biome-scale

distinctiveness informs broad conservation prioritization, while local-scale metrics guide site-level actions such as restoration, connectivity design, or invasive species control.

To translate these scale effects into spatial conservation priorities, we used functional rarity weighted richness to identify hotspots across scales. Rather than introducing a new conservation criterion, this approach operationalizes functional rarity within a well-established class of weighted richness metrics used in spatial prioritization (Albuquerque & Beier, 2015). The low spatial congruence of hotspots across scales mirrors patterns reported for phylogenetic endemism (Daru et al., 2020) and highlights a key implication: conservation strategies based solely on globally computed rarity metrics are likely to overlook areas that are functionally important at regional or local levels. Conversely, some globally prominent hotspots may lose priority when evaluated within finer-scale ecological contexts. These results clarify an important conceptual gap in functional biogeography: while the scaling of rarity components is well understood individually, how these scaling relationships combine within functional rarity—and how this combination propagates into spatial conservation prioritization—has remained largely unexplored. By explicitly tracing this propagation across four nested spatial scales, our study moves beyond documenting scale dependence to identifying where and why conservation priorities diverge across decision contexts.

Mapping areas of hotspot overlap reveals where conservation priorities converge across scales, notably in regions such as the tropical Andes, the East Afromontane, the Himalayas, and the Philippines. These areas represent robust priorities because they simultaneously maximize functional rarity under multiple spatial framings. More broadly, our results demonstrate that any integrative index combining trait-based rarity with geographic risk—such as FUSE (Griffin et al., 2020; Pimiento et al., 2023) or other originality–endangerment composites (Pavoine & Ricotta, 2024)—will inherit the scale sensitivity of its trait component. Recognizing this dependence is therefore essential for transparent interpretation rather than a limitation of the indices themselves. Practically, we recommend (i) computing the trait component at the decision-relevant scale (biome/realm for broad prioritization; local for site design), (ii) reporting both distinctiveness and uniqueness where feasible, and (iii) presenting parallel hotspot maps at two scales to reveal robust vs. scale-contingent priorities. This framing clarifies complementarity rather than redundancy among indices.

Our study brings four key messages for functional biogeography and conservation planning: (i) Functional rarity is inherently scale-dependent, but its components are not: geographic restrictedness varies strongly with scale, whereas trait distinctiveness remains comparatively robust and thus more suitable for broad-scale prioritization. (ii) Scale dependence should be viewed as an expected consequence of macroecological scaling laws rather than a methodological limitation, with critical implications for how functional rarity are interpreted. (iii) Spatial conservation priorities based on functional rarity show limited congruence across scales, indicating that global assessments alone are insufficient to capture regionally and locally important functional diversity. (iv) Effective conservation strategies therefore require a multi-scale, functionally informed framework that aligns trait-based metrics with the spatial scale of decision-making, distinguishing robust priorities from scale-contingent ones.

Rather than relying exclusively on globally computed rarity metrics, conservation strategies will thus benefit from explicitly integrating information across spatial scales to ensure that both globally unique and locally critical sites are represented. This integration is particularly relevant in the context of ambitious policy targets such as the Kunming–Montreal Global Biodiversity Framework (Kunming–Montreal Global Biodiversity Framework, 2022), where the central challenge is not only how much area to protect, but which dimensions of biodiversity to prioritize, and at which scales. Explicitly accounting for scale dependence in functional rarity offers a pragmatic way to reduce spatial mismatches between protection and functional diversity, thereby improving the effectiveness and resilience of conservation investments.

Code and data availability

All code and derived datasets generated in this study—including species-level distinctiveness, restrictedness and functional rarity at four spatial grains; gridded functional-rarity-weighted richness (Frwr) layers; hotspot masks; and figure-reproduction scripts—are archived at Zenodo (DOI:<https://doi.org/10.5281/zenodo.17513832>). Input trait and range data are from the AVONET database (Tobias et al., 2022) and are openly available from the original repository <https://figshare.com/s/b990722d72a26b5bfead>. Realm/biome boundaries are from WWF Terrestrial Ecoregions, and protected-area polygons are from the World Database on Protected Areas (August 2023 release) and available via Protected Planet under standard terms of use. No new field data were collected.

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Data Accessibility Statement

All code and derived datasets generated in this study—including species-level distinctiveness, restrictedness and functional rarity at four spatial grains; gridded functional-rarity-weighted richness (Frwr) layers; hotspot masks; and figure-reproduction scripts—are archived at Zenodo (DOI:<https://doi.org/10.5281/zenodo.17513832>). Input trait and range data are from the AVONET database (Tobias et al., 2022) and are openly available from the original repository. Realm/biome boundaries are from WWF Terrestrial Ecoregions, and protected-area polygons are from the World Database on Protected Areas (August 2023 release) and available via Protected Planet under standard terms of use. No new field data were collected.

Appendices

1. Trait distribution and correlations

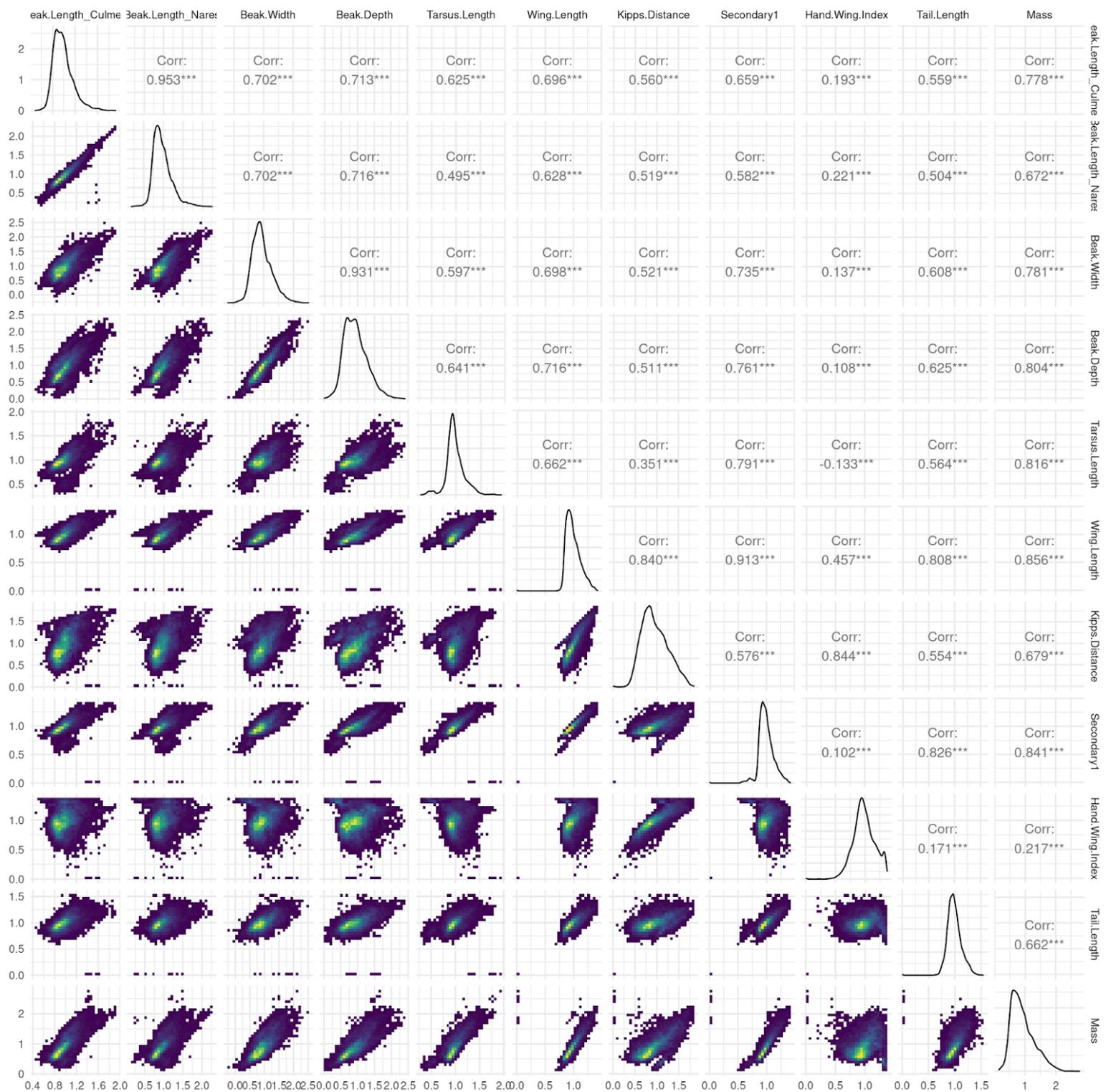


Figure A1. Pairwise relationships among the 11 log₁₀-transformed morphological traits used to construct avian trait space. Diagonal panels show trait distributions; lower panels show bivariate relationships across species; correlation coefficients are reported in the upper panels.

2.List of biomes and realms combinations

Realm	Biome	Realm/Biome intersect
Antarctica	Tundra	AN11
Australasia	Tropical & Subtropical Moist Broadleaf Forests	AU01
Palaearctic	Mediterranean Forests, Woodlands & Scrub	PA12
Palaearctic	Deserts & Xeric Shrublands	PA13
Nearctic	Tundra	NE11
Palaearctic	Temperate Grasslands, Savannas & Shrublands	PA08
Nearctic	Boreal Forests/Taiga	NE06
Afrotropic	Mediterranean Forests, Woodlands & Scrub	AF12
Nearctic	Temperate Conifer Forests	NE05
Afrotropic	Tropical & Subtropical Moist Broadleaf Forests	AF01
Afrotropic	Deserts & Xeric Shrublands	AF13
Nearctic	Temperate Broadleaf & Mixed Forests	NE04
Palaearctic	Temperate Conifer Forests	PA05
Palaearctic	Montane Grasslands & Shrublands	PA10
Neotropic	Tropical & Subtropical Moist Broadleaf Forests	NO01
Neotropic	Mangroves	NO14
Afrotropic	Temperate Grasslands, Savannas & Shrublands	AF08
Palaearctic	Flooded Grasslands & Savannas	PA09
Indomalayan	Tropical & Subtropical Moist Broadleaf Forests	IN01
Afrotropic	Montane Grasslands & Shrublands	AF10
Afrotropic	Tropical & Subtropical Grasslands, Savannas & Shrublands	AF07
Australasia	Tundra	AU11
Palaearctic	Temperate Broadleaf & Mixed Forests	PA04
Neotropic	Tropical & Subtropical Dry Broadleaf Forests	NO02
Neotropic	Deserts & Xeric Shrublands	NO13
Palaearctic	Tundra	PA11
Australasia	Tropical & Subtropical Grasslands, Savannas & Shrublands	AU07
Australasia	Montane Grasslands & Shrublands	AU10
Nearctic	Deserts & Xeric Shrublands	NE13
Neotropic	Tropical & Subtropical Grasslands, Savannas & Shrublands	NO07
Nearctic	Tropical & Subtropical Coniferous Forests	NE03
Nearctic	Temperate Grasslands, Savannas & Shrublands	NE08
Nearctic	Mediterranean Forests, Woodlands & Scrub	NE12
Australasia	Temperate Grasslands, Savannas & Shrublands	AU08
Afrotropic	Tropical & Subtropical Dry Broadleaf Forests	AF02
Australasia	Deserts & Xeric Shrublands	AU13
Oceania	Tropical & Subtropical Moist Broadleaf Forests	OC01
Afrotropic	Mangroves	AF14
Neotropic	Tropical & Subtropical Coniferous Forests	NO03
Neotropic	Montane Grasslands & Shrublands	NO10
Indomalayan	Tropical & Subtropical Dry Broadleaf Forests	IN02
Australasia	Temperate Broadleaf & Mixed Forests	AU04

Realm	Biome	Realm/Biome intersect
Antarctica	Tundra	AN11
Neotropic	Mediterranean Forests, Woodlands & Scrub	NO12
Australasia	Mediterranean Forests, Woodlands & Scrub	AU12
Neotropic	Flooded Grasslands & Savannas	NO09
Indomalayan	Deserts & Xeric Shrublands	IN13
Afrotropic	Flooded Grasslands & Savannas	AF09
Palaearctic	Boreal Forests/Taiga	PA06
Indomalayan	Temperate Broadleaf & Mixed Forests	IN04
Indomalayan	Temperate Conifer Forests	IN05
Neotropic	Temperate Grasslands, Savannas & Shrublands	NO08
Oceania	Tropical & Subtropical Dry Broadleaf Forests	NO02
Palaearctic	Tropical & Subtropical Moist Broadleaf Forests	PA01
Oceania	Tropical & Subtropical Grasslands, Savannas & Shrublands	NO07
Indomalayan	Tropical & Subtropical Coniferous Forests	IN03
Indomalayan	Mangroves	IN14
Neotropic	Temperate Broadleaf & Mixed Forests	NO04
Australasia	Tropical & Subtropical Dry Broadleaf Forests	AU02
Australasia	Mangroves	AU14
Indomalayan	Flooded Grasslands & Savannas	IN09
Afrotropic	Deserts & Xeric Shrublands	AF07
Nearctic	Tropical & Subtropical Dry Broadleaf Forests	NE02
Indomalayan	Tropical & Subtropical Grasslands, Savannas & Shrublands	IN07
Nearctic	Tropical & Subtropical Grasslands, Savannas & Shrublands	NE07
Indomalayan	Montane Grasslands & Shrublands	IN10

Table A2. List of WWF biomes intersected with WWF biogeographic realms used to define “biome-within-realm” analytical units (n = 66). For each unit, the table reports realm, biome name, and the realm/biome intersect identifier used in analyses.

3. Transformations

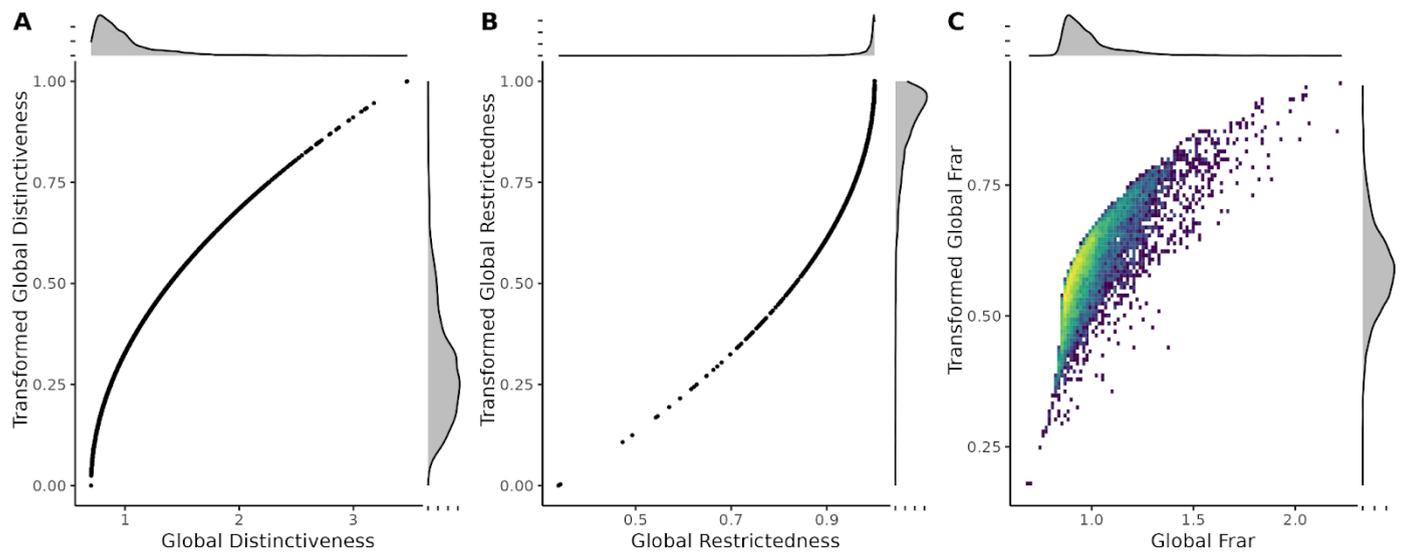


Figure A3. Monotonic transformations applied to (A) trait distinctiveness and (B) geographic restrictedness to reduce skewness and enable comparability across scales, and (C) the resulting relationship between transformed components and functional rarity (Frar).

4- Relationship between Frwr and species richness

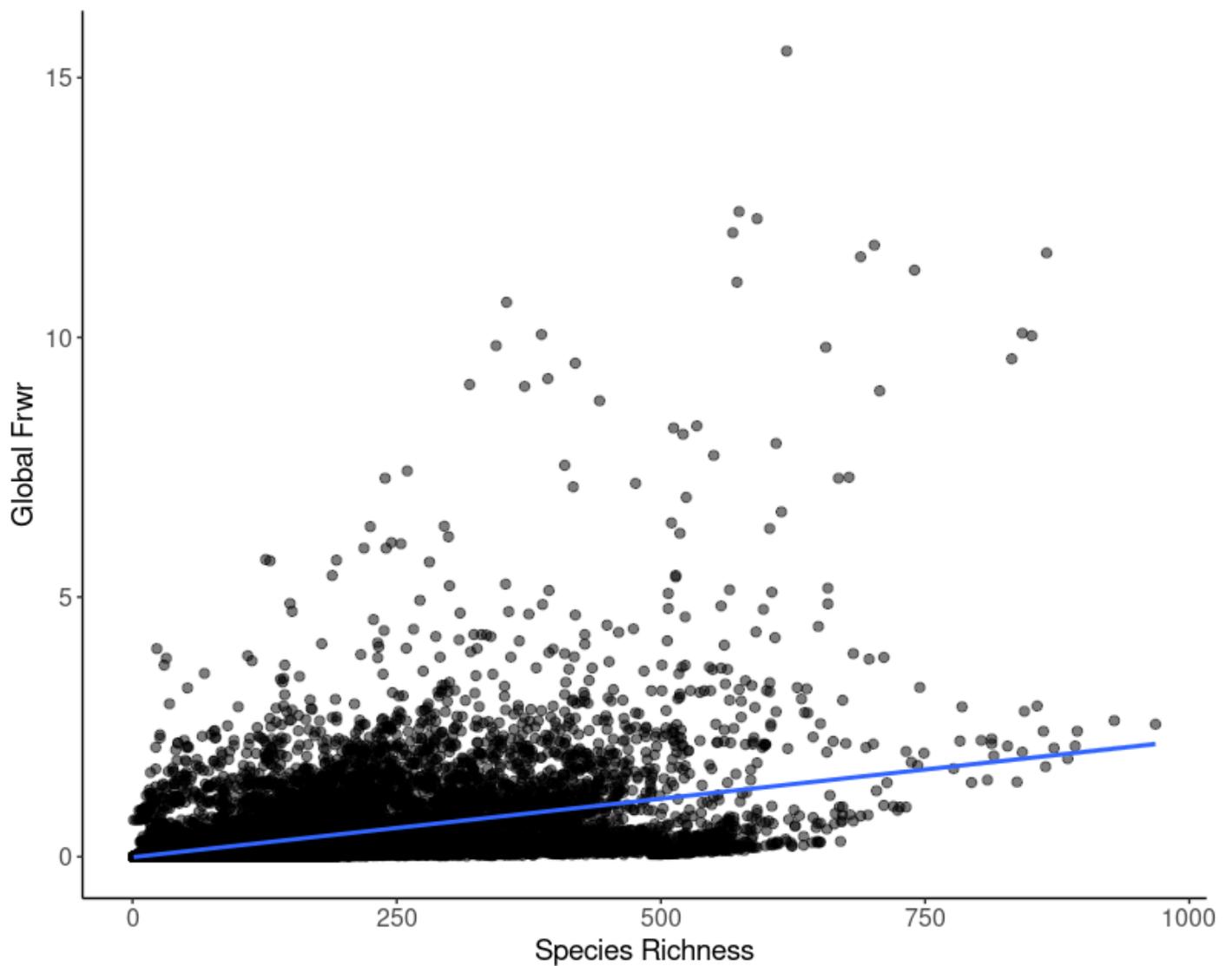


Figure A4. Relationship between functional rarity-weighted richness (Frwr) and species richness across global terrestrial grid cells. The dispersion around the main trend illustrates that assemblages with similar richness can differ substantially in Frwr due to differences in the contribution of functionally rare species.

5. Variation of distinctiveness mapped into morphological space

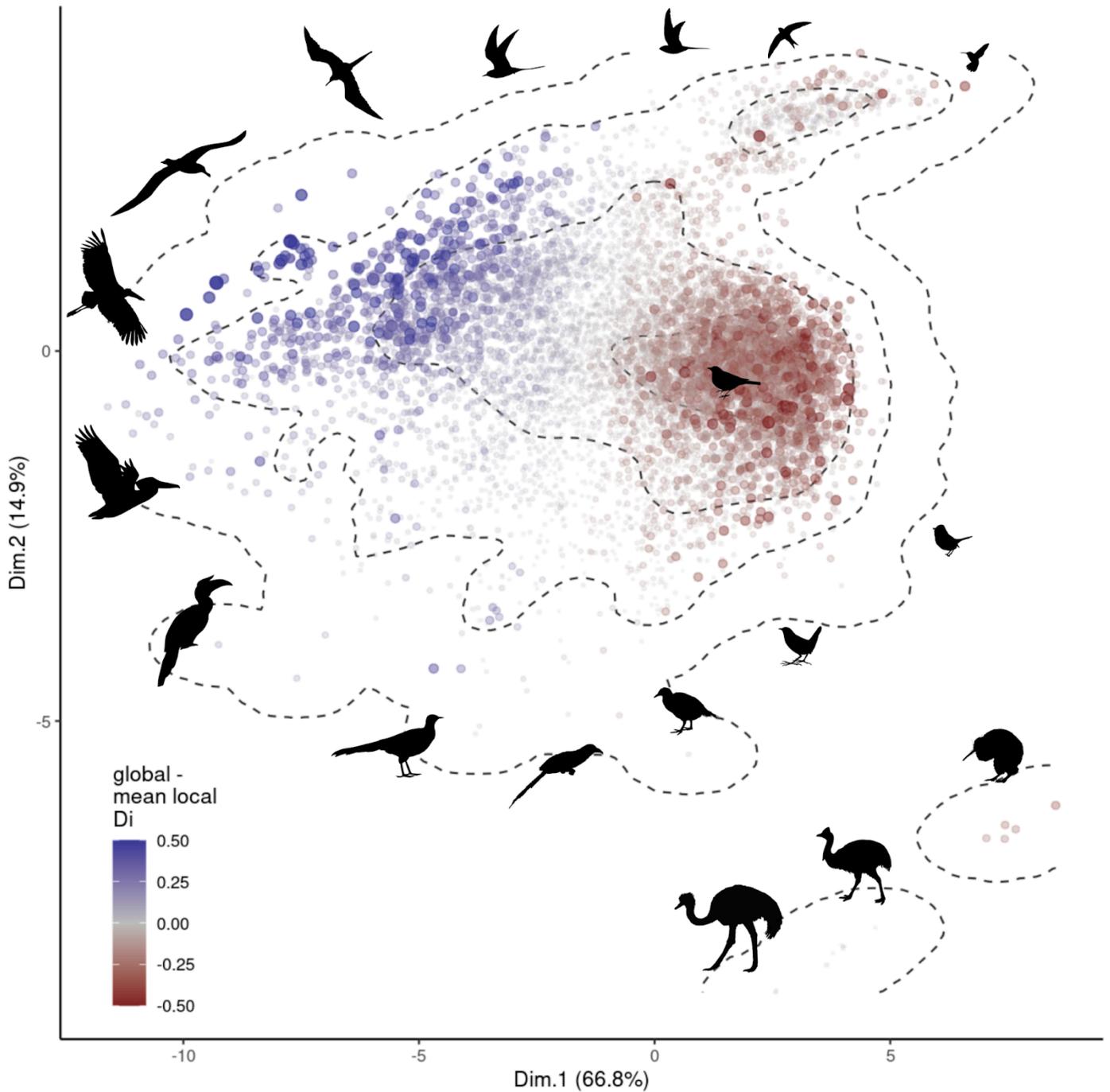


Figure A5. Difference between global and local trait distinctiveness (D_i) mapped in avian morphospace (first two PCA axes of the 11-trait space). Positive and negative values indicate species that are more distinct globally versus locally, illustrating how changes in reference pool composition modulate distinctiveness.