

Communication

# Spatial Patterns in the Morphological Diversity of Madagascan Frogs

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**Abstract:** Madagascar is a biodiversity hotspot, containing a large proportion of endemic species. To make conservation efforts more effective, it is necessary to understand the spatial distribution of this huge biodiversity. In this study, the patterns of morphological variation and diversity in the adult anurans of Madagascar were evaluated and compared across different climatic regions. These patterns were investigated for 370 species (2360 specimens), and the variation in 13 morphological traits obtained from taxonomic databases was assessed. The results revealed differences in body size distribution across climatic regions and that the most morphologically distinctive species occur in humid regions. The analysis also showed that anuran assemblages tend to be more species-rich, more morphologically diverse, and more morphologically clustered in tropical rainforests. These patterns are attributable to regional variations in the amount and seasonality of precipitation. An understanding of the complex patterns of spatial diversity could be useful for regional prioritization in the conservation of Madagascan anurans.

**Keywords:** amphibians; evolution; diversity hotspot; island; hotspot; tropical ecology



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## 1. Introduction

The study of the spatial variability in biodiversity has important implications for defining optimal conservation strategies, especially in those regions where there is evidence of habitat loss and where areas of valuable biodiversity must be identified rapidly [1]. The biotic communities of humid tropical regions are usually characterized by their high species richness, but other factors must be considered when defining potential priority areas for conservation, such as the phylogenetic and trait diversity of the species present in the candidate areas [2].

Biodiversity loss is one of the fundamental concerns of the current conservation efforts not only for the direct decline but because the effects on the ecological functioning of the ecosystems could imply deep consequences [3–5]. The resilience of the ecosystems after biodiversity loss has been recognized as one of the central goals of both community and ecosystem ecology, and several concepts, mechanisms and theories have long been developed: among them, “functional redundancy” [6,7]. Functional redundancy is hypothesized to promote ecological resilience. Thus, communities with more redundant species (those that perform similar ecological functions) should be buffered against the loss of individual species. However, the wideness of this concept requests more evident-based studies [8], because limited functional redundancy has been observed even in some high biodiversity communities, where high functional redundancy is expected [9]. In this sense, the studies of potential functional redundancy (using morphological traits as a proxy to evaluate functional traits) in rich communities could provide important insights, e.g., [10–12]. For all of this, the study of the patterns of spatial trait distribution provides pivotal knowledge to better understand community resilience.

The trait diversity among biotic assemblages is estimated by measuring several shared external descriptors that are potentially useful in evaluating interspecific interactions

and species' niche preferences or as surrogates of their evolutionary relationships [13,14]. Some of these traits may also be functional if they are associated with a higher chance of survival or the reproductive success of the species [15]. However, this categorization can be subjective, particularly in groups whose ecology and phenology are not accurately known [16,17]. Trait diversity can be measured using various indices, which assess the level of morphological divergence among species and the ranges of trait variations [18].

Madagascar is considered one of the most important of the world's biodiversity hotspots, with several new species being described each year [19–21]. Moreover, most of those species are strictly endemic, and some occur in small, isolated and unprotected patches [22,23]. In this context, it is crucial to enhance the knowledge of Malagasy species in order to prioritize conservation measures in the most vulnerable regions.

In this study, the variation in the diversity of morphological traits among several macro-assemblages of anurans from Madagascar was evaluated. This island is a hotspot of biodiversity and contains numerous endemic lineages because it has long been isolated from continental landmasses (since 100–80.3 Ma [24,25]). Anurans also account for many endemic radiations, with about 370 described species (a number increasing at a rapid pace) [26], which are distributed throughout all the biomes of the island. However, the species are unevenly distributed, which could be attributed in some cases to recent range contractions induced by rapid environmental deterioration [27]. Therefore, investigating the spatial patterns of anuran diversity in Madagascar must remain a priority, because this group is severely threatened by the progressive degradation of its habitats, illegal trade, emerging diseases, and the expansion of alien species [28–31].

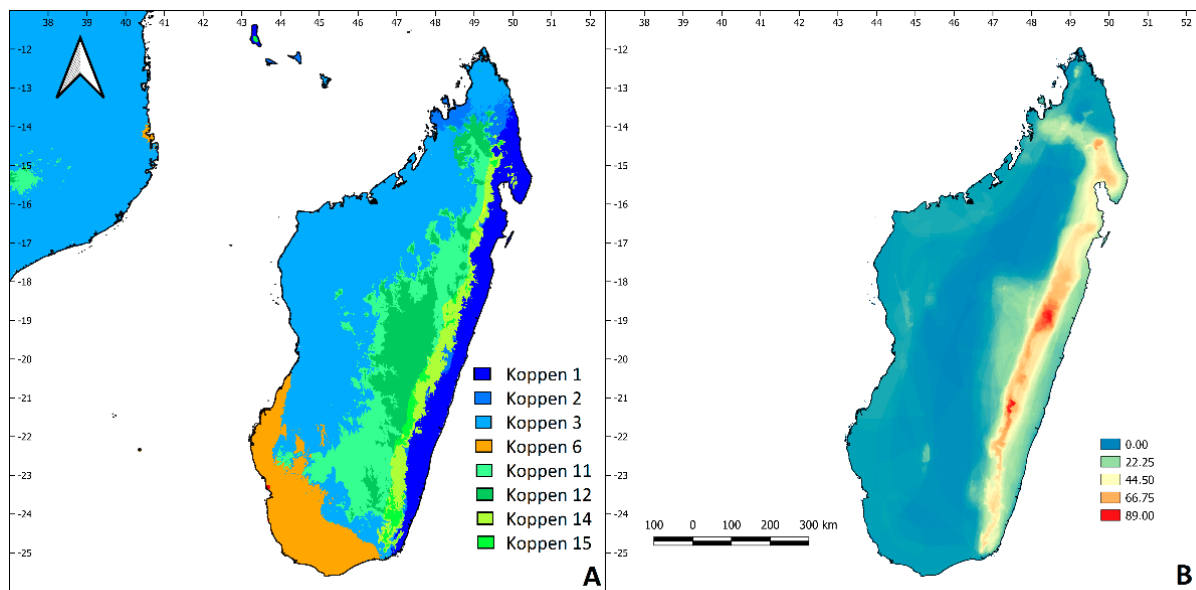
The trait diversity among anuran assemblages in Madagascar has been evaluated in several climatic regions, which are defined by the Köppen–Geiger system [32]. This classification is mainly designed to assess the global distribution of vegetation and is therefore widely used to study large-scale patterns of biotic diversity, including amphibian distributions [33,34]. According to the Köppen–Geiger classification, the climate in Madagascar is grouped into tropical subtypes (humid to arid, structured along a northeast–southwest axis), with an orographic gradient toward humid subtropical–temperate climates in the central highlands [35]. Similar to other regions of the globe, the vegetation biomes in Madagascar fit into these Köppen categories [36].

Variations in the species compositions of anuran assemblages among Köppen regions have been used to test two hypotheses about the causes underlying their morphological variability [37]. Milder environmental conditions (such as in the humid tropics) should facilitate a greater range of morphological diversification (hypothesis i) because the species should be able to occupy a broader range of niches [38]). Moreover, the assemblages in the humid tropics could be more morphologically clustered (hypothesis ii) because highly productive and environmentally stable habitats favour closer species packing) [39].

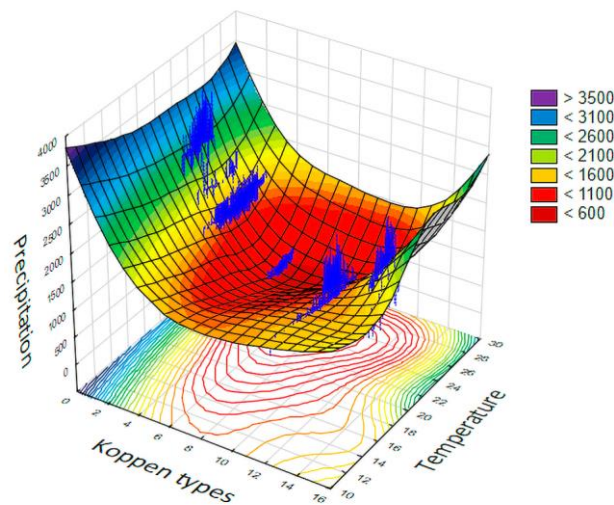
## 2. Materials and Methods

### 2.1. Study Region

The study region was the island of Madagascar (southwestern Indian Ocean; 587,041 km<sup>2</sup>). The island displays remarkable climatic heterogeneity and very rich assemblages of amphibians (Figure 1). The climate types are Köppen 1 (climate = Af, tropical rainforest; 63,656 km<sup>2</sup>, biome = evergreen rainforest), Köppen 2 (Am, tropical monsoon; 14,552 km<sup>2</sup>, Sambirano rainforest), Köppen 3 (Aw, tropical savannah; 256,715 km<sup>2</sup>, dry deciduous forest), Köppen 6 (BSh, arid hot steppe; 66,499 km<sup>2</sup>, arid spiny bush), and the highland climates: Köppen 11 (Cwa, temperate, dry winter–hot summer; 86,616 km<sup>2</sup>), Köppen 12 (Cwb, temperate dry winter–warm summer; 62,898 km<sup>2</sup>), Köppen 14 (Cfa, temperate, no dry season–hot summer; 32,531 km<sup>2</sup>), and Köppen 15 (Cfb, temperate, no dry season–warm summer; 8783 km<sup>2</sup>) [20]. The mean values for the mean annual temperature, accumulated annual precipitation (Figure 2), and precipitation seasonality for each of these Köppen categories were obtained from the WorldClim2 database [40], using Quantum-GIS [41].



**Figure 1.** Köppen climatic regions (A) and anuran species richness (B) in Madagascar. In panel B, warmer colors indicate greater species richness. Köppen regions are based on Beck et al. (2018) [35] and species richness was generated from IUCN range polygons (2023). The north arrow (A) indicates the direction of north.



**Figure 2.** Climatic variability in Madagascar. The figure shows the variations in the mean annual temperature ( $^{\circ}\text{C}$ ) and the accumulated rainfall per year (mm) according to the Köppen types or regions. Blue lines indicate the distributions of climatic values for each Köppen region.

## 2.2. Species Data

The data on the distributions of species were based on the International Union for Conservation of Nature (IUCN) distribution polygons [42] except for a few species for which these polygons were not available and for which occurrence data were obtained from the type localities. The presence of each species within a climate type was determined by the intersection of the IUCN polygons, the Köppen types, and the terrain elevation, which restricted the occurrence of a species to the elevation ranges provided in the literature [42]. When a Köppen region represented <15% of the area of occurrence of a species, this region was discarded to prevent overestimates of the niche extent, which is an error that can arise in data generated with range polygons [43].

The morphological features of the native species of frogs were obtained from taxonomic literature sources [44–50]. Most of the species descriptions had been produced by a small group of authors and therefore follow a homogeneous methodology. In total, data were collected for 2360 specimens of 370 species of frog (Supplementary Table S1). The morphological variables used to compute the diversity indices are shown in Table 1, and they included body size (snout–urostyle length; SUL) and 12 ordinal descriptors of relative hind-limb length, toe webbing, skin texture, and other characteristics. These characters were chosen based on their availability in the taxonomic descriptions, although some might be relevant to species fitness such as body size, toe webbing, digital tips, relative hind-limb length, and skin texture [51]. Dorsal colouration, although potentially important, was excluded because its inter-individual variability is high [44]. No frogs were handled or collected during the study, and the species data were collected only from literature databases.

**Table 1.** Species traits used in the study. For each trait, the range and an interpretation are shown.

Trait	Range	Interpretation	Trait	Range	Interpretation
Snout–urostyle length	8.0–125.6	Body size (mm)	Number of toes	3	Miniaturization
				4	Miniaturization
				5	Ancestral
Finger–pads	0 1 2	Absent Slightly enlarged Distinctly enlarged	Dorsal skin	0	Smooth–finely granular
				1	Disseminated tubercles–ridges
				2	Roughly granular
Hand webbing	0 1 2	Absent Reduced Developed	Supra–ocular tubercles	0	Absent
				1	Small
				2	Large
Foot webbing	0 1 2 3	Absent Reduced Developed Fully webbed	Limb tubercles	0	Absent
				1	Heel–elbow
				2	Arms–legs
				3	
Tibiotarsal joint reaching	0 1 2 3 4	Forelimb Tympanum Eye Nostril Snout tip	Ventral coloration	0	White/unpigmented
				1	Dark spotted
				2	Grey–amber
				3	Dark
				4	Intensely colored
Outer metatarsal tubercle	0 1	Absent Present	Pupils	0	Vertical
				1	Horizontal
				2	Horizontal indistinct
Femoral glands	0 1	Absent Present			

### 2.3. Data Analyses

The analyses evaluated (i) the variability in body size and in trait diversity across the Köppen regions, and (ii) the association between trait variability and climatic conditions. First, the distribution of body size (= SUL) for the species of Madagascar anurans was compared among the Köppen regions using density functions. This type of nonparametric analysis is suitable when a continuous variable does not follow a normal distribution [31], as in the case of SUL (Shapiro–Wilk  $W = 0.812$ ,  $p = 2.48 \times 10^{-56}$ ). The pairwise differences were determined with equality tests [52], and the  $p$ -values were adjusted for multiple comparisons using the standard Bonferroni correction [53]. This analysis was performed using the *sm* package [54] in the R environment [55].

Then, the spatial variation in trait diversity was investigated. Three diversity indices were estimated: one was estimated directly from the trait matrix, the species distinctiveness

(SD), and the other two evaluated the differences between the observed patterns and those expected under the null distribution, i.e., Faith's diversity (PD) and the mean pairwise distances (MPD). In both indices, the standardized effect size was also estimated: the standardized effect size of Faith's diversity (SES PD) and the standardized effect size of the mean pairwise distances (SES MPD), respectively [56–58]. These diversity indices were chosen because they are computed from distance matrices and tolerate cases with missing values [59]. SD measures whether a species is more or less similar in its traits to another species [58]. This index was calculated from Gower distances [60] because the trait matrix includes both quantitative and ordinal variables. To build these distance matrices, greater weight was assigned to quantitative variables than to ordinal ones [61]. The distance matrices were constructed after 10,000 resamplings, thus avoiding the error associated with estimates based only on measures of the central tendency of the species [62]. These analyses were performed using the *funrar* package [63] in R.

The variability in the diversity patterns was evaluated by estimating SES PD and SES MPD. These metrics estimate the diversity of an assemblage irrespective of the species richness [42]. SES PD is an indicator of trait richness and assesses whether there is an underdispersion (negative SES and  $p < 0.05$ ) or overdispersion (positive SES and  $p > 0.95$ ) of traits in a group of species [63]. SES MPD is an indicator of species divergence and assesses whether the species that form an assemblage are morphologically clustered (positive SES and  $p > 0.95$ ) or overdispersed (negative SES and  $p < 0.05$ ). Thus, for a given number of species, positive values of SES MPD are related to higher redundancy than negative ones [63]. The statistical significance of the differences between the observed and expected values was obtained after 1000 randomizations generated with an independent swap algorithm [63]. These analyses were performed using the package *picante* [63] in R. The diversity indices were correlated with the climatic mean values for the Köppen climatic regions (mean annual temperature, accumulated precipitation, and seasonality of precipitation) using Spearman's rank-order correlation coefficient [64].

### 3. Results

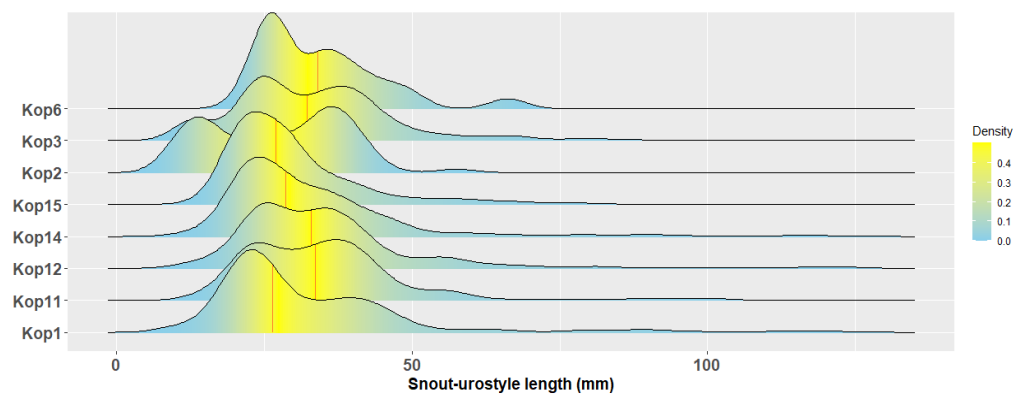
The results of the test of equality between two density functions revealed that the distribution of body size was not homogeneous across the Köppen regions (Table 2), although most of the measured specimens were between 25 and 50 mm SUL in all regions (Figure 3).

**Table 2.** Results of the test of equality between densities (Bonferroni adjusted  $p$ -values), comparing the distribution of the snout–urostyle length for different species of Madagascar frogs. Kop, Köppen types.

	Kop1	Kop2	Kop3	Kop6	Kop11	Kop12	Kop14
Kop1							
Kop2	0.0						
Kop3	0.0	0.0					
Kop6	0.700	0.196	1.00				
Kop11	0.0	0.0	1.00	1.00			
Kop12	0.0	0.0	1.00	1.00	1.00		
Kop14	0.0	0.0	0.0	1.00	0.0	0.0	
Kop15	0.0	0.0	0.0	0.308	0.0	0.0	0.0

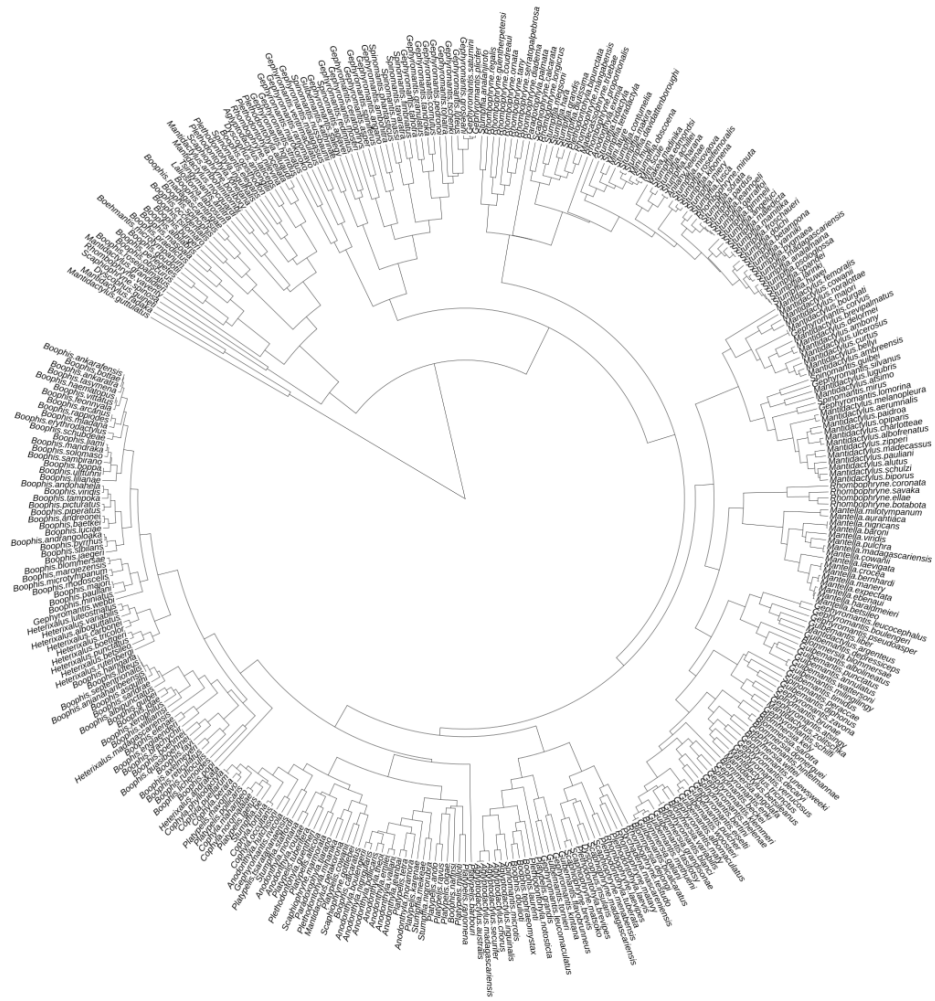
The tree generated from the Gower distance matrix is shown in Figure 4 and identifies genera with greater morphological divergence, such as *Mantidactylus* and *Boophis*, whereas the other taxonomic groups are more morphologically uniform (Figure 4). The estimates of species distinctiveness showed that morphologically very distinctive species occur in Köppen regions 1, 12, and 14 (Figure 5). The analysis indicated that SES Faith's PD was smaller than expected in Köppen regions 2 and 3 (trait underdispersion), and these results were highly significant (Table 3). The SES MPD values indicated that the species

tended to be morphologically clustered in Köppen region 1 and overdispersed in Köppen regions 15 and 6, although the results for these latter regions were not highly significant (Table 4). The results of Spearman's correlation revealed that these patterns of variability are attributable to an effect of precipitation rather than of temperature. In this sense, the amount of precipitation was positively associated with the presence of morphologically distinctive species (95th percentile of SD) and with species-rich and morphologically clustered assemblages (Table 5).

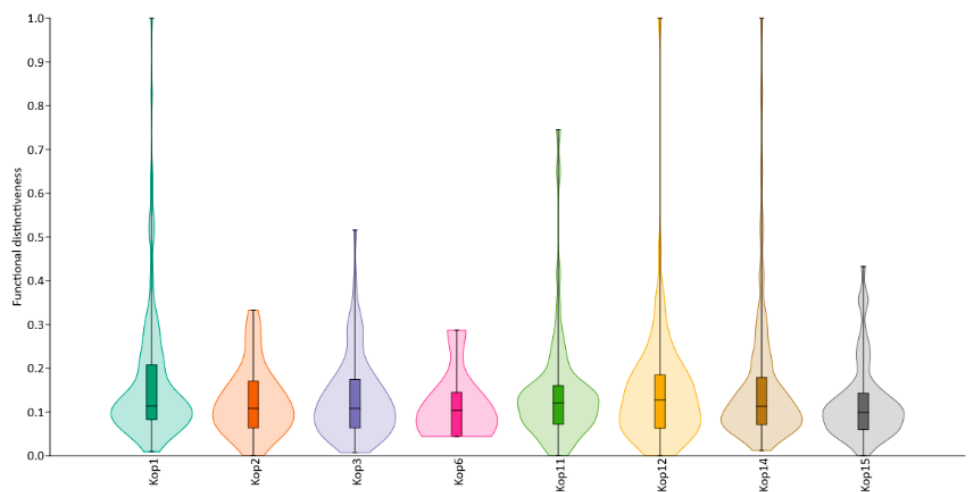


**Figure 3.** Representation of body size variability in Madagascan frogs across Köppen (Kop) regions. Lines represent density functions, and the red line represents the median value for the snout–vent length.





**Figure 4.** Trait diversity tree plot, representing the similarities among the anuran species in Madagascar, based on 13 morphological traits.



**Figure 5.** Violin density plots, showing the variability in trait distinctiveness in the anuran species across Köppen regions. The box represents the 25–75 quartiles, and the violin shape represents the kernel density plot, ranging from the maximum value to the minimum value. Köppen regions are separated by distinctive colors.

**Table 3.** Estimation of Faith’s trait diversity (PD) metric, standardized effect size of Faith’s diversity (SES PD) and its statistical significance ( $p$ ). The percentages indicate the proportion of results in which the  $p$ -value (quantile) of observed PD vs. null communities was  $<0.05$  or  $>0.95$  after 1000 resamplings. N taxa, number of species. Positive values in SES PD indicate greater functional richness.

	N Taxa	PD	SES PD	$p < 0.05\%$	$p > 0.95\%$
Köppen 1	129	4.472	1.295	0.0	26.2
Köppen 2	27	1.309	−2.518	98.2	0.0
Köppen 3	76	2.764	−2.465	95.0	0.0
Köppen 6	7	0.621	−0.680	8.4	0.0
Köppen 11	61	2.715	−0.122	0.0	0.0
Köppen12	82	3.412	0.915	0.0	6.2
Köppen 14	150	4.815	0.996	0.0	7.8
Köppen 15	65	2.684	−1.085	15.3	0.0

**Table 4.** Estimation of mean pairwise distances (MPD) metric, standardized effect size of mean pairwise distances (SES MPD) and its statistical significance ( $p$ ). The percentages indicate the proportion of results in which the  $p$ -value (quantile) of observed MPD vs. null communities was  $<0.05$  or  $>0.95$  after 1000 resamplings. N taxa, number of species. Positive values in SES MPD indicate greater trait clustering.

	N Taxa	MPD	SES MPD	$p < 0.05\%$	$p > 0.95\%$
Köppen 1	129	0.208	2.615	0.0	99.8
Köppen 2	27	0.176	−0.796	0.0	0.0
Köppen 3	76	0.179	−1.190	8.5	0.0
Köppen 6	7	0.137	−1.331	49.0	0.0
Köppen 11	61	0.186	−0.461	0.0	0.0
Köppen12	82	0.191	0.014	0.0	0.0
Köppen 14	150	0.195	0.766	0.0	0.0
Köppen 15	65	0.172	−1.749	65.7	0.0

**Table 5.** Spearman’s coefficient ( $r_s$ ) evaluating the correlation between two climatic variables (annual mean temperature and accumulated precipitation per year) and the diversity indices. N taxa, number of species; FD, trait distinctiveness; SES PD, standardized effect size of Faith’s diversity; SES MPD, standardized effect size of mean pairwise distances. Statistically significant associations are shown in bold (alpha = 0.1).

		Temperature	Precipitation	Prec. Seasonality
N Taxa	Spearman’s $r_s$	−0.405	<b>0.670</b>	−0.524
	$p$	0.329	<b>0.069</b>	0.197
Mean SUL	Spearman’s $r_s$	−0.286	−0.478	0.151
	$p$	0.501	0.231	0.571
Mean FD	Spearman’s $r_s$	−0.286	<b>0.693</b>	−0.452
	$p$	0.501	<b>0.057</b>	0.267
P95 FD	Spearman’s $r_s$	−0.149	<b>0.746</b>	<b>−0.671</b>
	$p$	0.725	<b>0.035</b>	<b>0.075</b>
SES PD	Spearman’s $r_s$	−0.495	0.278	−0.524
	$p$	0.213	0.504	0.197
SES MPD	Spearman’s $r_s$	0.021	<b>0.740</b>	−0.476
	$p$	0.961	<b>0.036</b>	0.243

#### 4. Discussion

In this study, the spatial patterns of morphological diversity among the adult forms of anurans in Madagascar were evaluated for the first time. The analyses revealed important



differences in the morphological diversity across the main climatic regions, which can be attributed largely to variations in the amount and seasonality of precipitation. Equality tests are sensitive to variations in the extremes of density curves [52]; therefore, the test differences imply that the relative frequencies of body sizes are distributed non-homogeneously across the Köppen regions throughout Madagascar. This result suggests that certain ranges of size are likely to be more adaptive in some climate zones; for example, larger sizes may be more adaptive in drier regions.

Trait richness showed remarkable variation in tropical regions, decreasing significantly under the drier and seasonal conditions in Köppen regions 2 and 3. Although it cannot be completely ruled out that in Köppen 2 region, where may also be a consequence of its relatively small geographic extent, this result indicates that the amount of rainfall limits the morphological diversification of Madagascan anurans. Therefore, the Madagascan anuran assemblages tend to be more species-rich, more morphologically diverse, and more morphologically clustered in its tropical rainforests. In other words, the assemblages with higher species richness tend to show higher morphological redundancy.

Many species of tropical amphibians show low tolerance for wide variations in ambient temperature and relative humidity, and species richness tends to be higher where these fluctuations are smaller [65]. Greater species richness may also be facilitated by closer species packing, perhaps as a consequence of higher biomass productivity [66] or the ability of these frogs to efficiently exploit the three-dimensional structure of rainforest habitats [67,68]. The origin of the tropical rainforests in eastern Madagascar may date back to the Eocene, and this long-term stability may underlie the enormous biotic diversity of these forests [69]. In the case of anurans, these long periods of evolution may also have increased their opportunities for adaptive radiation both in their adult and larval forms [70].

Our results were probably influenced by the morphological traits selected for the study and the presence of some missing values. The morphological traits examined in the taxonomic descriptions were those available in the literature, although some were thought to be functionally relevant (e.g., body size, relative hind-limb length, and skin texture). Additional studies will be required in the future to verify the results of this study, with traits selected expressly for their functional roles, and the patterns of diversity within and outside postulated rainforest glacial refugia should be compared [71]. This approach will provide greater insight into the environmental drivers that regulate the biodiversity in these extremely rich tropical anuran assemblages, including the historical evolution of their forest habitats [71].

Currently, most conservation plans are solely focused on generic indicators such as species richness without considering other dimensions of biodiversity or even species threats [72–74]. The information provided by this study could easily be implemented when designing conservation strategies, having a direct impact on the efficiency of the resources invested in amphibian conservation or even protecting the most singular regions.

## 5. Conclusions

Consistent patterns of species richness and morphological diversity on the island of Madagascar have been identified, and these are particularly marked in the eastern tropical rainforests of the island. Assemblages with high morphological redundancy are potentially more resistant to environmental changes and biological invasions, favouring the preservation of unique evolutionary lineages [75]. Therefore, the protection of rainforests must be a priority for the conservation of amphibians in Madagascar, as has already been indicated for other groups of vertebrates on this island, including chameleons and lemurs [76,77]. Focusing on the methods used to calculate diversity metrics, the results of the present study emphasize the potential utility of taxonomic databases for exploratory studies of patterns of diversity in highly diverse tropical communities.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/ecologies4030032/s1>, Table S1: Morphological traits of the species included in the study.

**Author Contributions:** Conceptualization, D.E.; methodology, D.E.; software, D.E.; validation, D.E.; formal analysis, D.E.; investigation, D.E.; resources, D.E.; data curation, D.E. and S.P.; writing—original draft preparation, D.E. and S.P.; writing—review and editing, D.E., S.P. and D.B.; visualization, D.E.; supervision, D.E. and D.B.; project administration, D.E. and D.B. All authors have read and agreed to the published version of the manuscript.

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