Article

The Effect of Climate and Human Pressures on Functional Diversity and Species Richness Patterns of Amphibians, Reptiles and Mammals in Europe

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Abstract: The ongoing biodiversity crisis reinforces the urgent need to unravel diversity patterns and the underlying processes shaping them. Although taxonomic diversity has been extensively studied and is considered the common currency, simultaneously conserving other facets of diversity (e.g., functional diversity) is critical to ensure ecosystem functioning and the provision of ecosystem services. Here, we explored the effect of key climatic factors (temperature, precipitation, temperature seasonality, and precipitation seasonality) and factors reflecting human pressures (agricultural land, urban land, land-cover diversity, and human population density) on the functional diversity (functional richness and Rao's quadratic entropy) and species richness of amphibians (68 species), reptiles (107 species), and mammals (176 species) in Europe. We explored the relationship between different predictors and diversity metrics using generalized additive mixed model analysis, to capture non-linear relationships and to account for spatial autocorrelation. We found that at this broad continental spatial scale, climatic variables exerted a significant effect on the functional diversity and species richness of all taxa. On the other hand, variables reflecting human pressures contributed significantly in the models even though their explanatory power was lower compared to climatic variables. In most cases, functional richness and Rao's quadratic entropy responded similarly to climate and human pressures. In conclusion, climate is the most influential factor in shaping both the functional diversity and species richness patterns of amphibians, reptiles, and mammals in Europe. However, incorporating factors reflecting human pressures complementary to climate could be conducive to us understanding the drivers of functional diversity and richness patterns.

Keywords: taxonomic diversity; functional richness; Rao's quadratic entropy; climatic variables; generalized additive mixed models; macroecological patterns; diversity drivers

1. Introduction

The multiple processes and factors acting simultaneously and shaping biodiversity patterns at different scales constitute a long-standing puzzle for ecologists and biogeographers [1,2]. Taxonomic diversity has been extensively used to unravel underlying mechanisms that structure communities and drive diversity patterns across scales [3]. However, other aspects of biodiversity such as functional diversity reflecting species' functional traits within communities and ecosystems [4] might provide a more detailed and integrated interpretation of diversity patterns and species composition [5,6]. Functional traits can be defined as the main dimensions of the real ecological niche [7], mediating species responses to environmental conditions and reflecting the way organisms respond to environmental variation (e.g., habitat or climate preference) [8]. Functional diversity is quantified by arranging species in a functional trait space according to their functional trait values [9]. This representation allows us to measure various aspects of functional diversity such as

functional richness (i.e., the overall volume of trait space (niche) occupied by species in a community) [10] or Rao's quadratic entropy (i.e., the functional distance between all pairs of species within a community) [9]. Therefore, the analysis of functional diversity patterns along environmental gradients, including land-use changes and human pressures, is a valuable tool to unlock the role of different factors shaping biodiversity patterns and to predict possible shifts in ecosystem functioning under the prism of global change [11].

Climate is a strong driver of species distributions and diversity patterns [10,12–15]. Research has shown that climatic stress gradients can limit functional diversity; for example, only species with certain adaptations can exist in harsh environmental conditions, and as a result, more functionally similar species coexist there [13,14,16,17]. On the other hand, climate seasonality can facilitate species coexistence despite their different ecological niches [18,19] or limit functional diversity when species with narrower niches coexist in areas of higher energy availability (and/or of lower environmental seasonality) [20,21]. Beyond climatic variables, landscape and contemporary human imprint play important roles in shaping species distributions [22] and functional diversity patterns [11,23]. A negative association between human imprint and functional diversity has been reported [24,25]; for example, highly urbanized communities show significantly decreased functional diversity in contrast to natural environments [26,27], while higher vulnerability characterizes functionally dissimilar species of intensified agricultural areas [28]. However, there are counterexamples which show that urban and agricultural land changes influence community structuring and thus functional diversity by favoring specific adaptations of species to cope with the new environments [11]. Yet, our understanding of the contribution of human pressures to large-scale patterns of functional diversity and their relative importance compared to other mechanisms such as climate remains fragmentary [11,23,29]. Furthermore, functional diversity patterns have generally been investigated in single taxonomic groups, despite the fact that different taxa may play similar and/or complementary ecological and functional roles [11,30]. Comparative analyses of the functional roles and functional diversity patterns of different taxonomic groups are scarce and focused primarily on local scales [11,26], while the same question for broad scales is still in its infancy (see [30]).

Functional traits and functional diversity infer a linkage between biodiversity and ecosystem functioning [31,32]. In this context, examining how functional diversity changes with environmental conditions can shed light on the impacts of climate, landscape, and human imprint on ecosystem processes. Here, we examine the taxonomic and functional diversity patterns of three taxonomic groups (amphibians, reptiles, and mammals) across Europe and explore the effect of climate (temperature, precipitation, temperature seasonality, and precipitation seasonality) and human pressures (agricultural and urban land area, land-cover diversity, and human population density) on their diversity patterns. Amphibians, reptiles, and mammals might either have similarities in key functional roles (e.g., amphibians and reptiles) or differ in ecological roles (mammals) while also having a direct link (e.g., one taxonomic group as a feeding resource for another). Given the scale and extent of our study, we expect that climate will have a stronger influence on these patterns [15,16] in contrast to the human pressures which mainly act at local scales ([11,23]; see [33]).

2. Materials and Methods

2.1. Species Distribution Data

We compiled distributional data for 68 amphibian species, 107 reptile species, and 176 mammal species in Europe (2488 grid cells) from two atlases, *The Atlas of European Amphibians and Reptiles* [34] and *The Atlas of European Mammals* [35]. Both atlases provide distributional presence/absence data on equal area grid cells of 50 km × 50 km, based on field surveys, published records, and national atlases projected on the WGS84 coordinate reference system.

2.2. Trait Data

We compiled trait datasets for amphibians, reptiles, and mammals in Europe using several available databases (published papers, books, electronic databases; Supplementary Material, Table S1). The selection of traits was based on the completeness of the availability of species' trait data and on their previous use in quantifying amphibian, reptile, and mammal functional diversity [19,29]. Our trait selection process resulted in the following five functional trait categories (with sub-categories): (a) body length (body mass for mammals), (b) clutch size (litter size for mammals and some viviparous amphibians and reptiles), (c) activity time (nocturnal, diurnal, crepuscular only for mammals), (d) diet type (herbivore, insectivore, molluscivore (only for amphibians and reptiles), carnivore, and omnivore), (e) habit (aquatic, fossorial, ground dwelling, and above-ground dwelling/arboreal). Traits a and b were considered as numerical variables, and traits c–e as binary variables.

2.3. Functional Diversity Indices

The functional diversity of each grid cell was estimated by metrics previously evaluated for their relationship with species richness [36], and amongst them [37] were (a) functional richness, defined by the convex hull volume occupied by the species of each grid cell; and (b) functional Rao's quadratic entropy, measured as the distance between two randomly selected species within the grid cell. We applied a Gower distance matrix to capture both the numeric and binary variables in our trait dataset and then performed principal coordinates analysis (PCoA) to ordinate species along the major axes and arrange them in a multidimensional functional trait space. Metrics were calculated using the "dbFD" function in the R package "FD" [38]. Furthermore, we estimated species richness per grid cell.

2.4. Environmental Data

Four climatic variables retrieved from the WorldClim climate database [39] (mean annual temperature, annual precipitation, temperature seasonality, and precipitation seasonality) and four variables related to human pressures (agricultural land area, urban land area, land-cover diversity, and population density) were investigated to understand their relationship with functional richness and Rao's quadratic entropy. Landscape data (agricultural land area, urban land area, and land-cover diversity) were provided by the land-cover dataset CLC2000 [40], and human population density was obtained from HYDE Gridded Population version 3.1 [41]. The environmental data were reprojected and resampled to the same projection and resolution as the distribution data in QGIS version 2.10.0.

2.5. Statistical Analysis

We applied generalized additive mixed models (GAMMs) with the "gamm" function of the "mgcv" R package [42], predicting the species richness and the functional diversity (functional richness and Rao's quadratic entropy separately) of amphibians, reptiles, and mammals as a function of the climatic predictors and those related to human pressures. Specifically, we built three models for each diversity metric: (a) a climatic model that included only climatic variables, (b) a land–human model including land-use-related variables and human population density, and (c) an overall model including all the predictors. We used Poisson error distribution for species richness and Gaussian error distribution for functional diversity indices. To account for spatial autocorrelation, we included the spatial correlation structure of coordinates (Gaussian distribution). All the predictors were modelled as smooth predictors with penalized thin plate regression splines, using three knots per spline. Prior to modelling, we checked for multicollinearity among variables by applying the variance inflation factor (VIF). Since all VIF values scored <10 [43], we included all variables in the model. Total precipitation and precipitation seasonality were square-root transformed and land-cover diversity, agricultural area extent, and human population density were log10 transformed prior to analysis to improve normality. Grid cells with less than 50% land-cover were excluded from the analysis.

3. Results

Species richness patterns varied across different taxonomic groups. Amphibians and mammals showed similar patterns with higher species richness in Central Europe, while reptiles followed a different pattern showing higher species richness in Southern Europe (Figure 1a–c). Amphibians and reptiles exhibited similar spatial patterns of functional richness in Europe, where they manifest a clear latitudinal pattern with the lowest functional richness values found in northern Europe, that is, regions with low temperatures (Figure 1d,e). Interestingly, arid areas along the coastline of Southeastern Europe were poorer in terms of functional richness for amphibians than for reptiles, with reptiles having the highest values in these regions. Contrastingly, mammal functional richness showed a more uniform pattern across Europe, with moderate to high functional richness values across all of Europe (Figure 1f). Lower values of mammal functional richness were found in the coastline of the Mediterranean region (Figure 1f). Rao's quadratic entropy patterns exhibited similar results, with those of functional richness patterns for all the three examined taxa showing high and significant associations (amphibians: $R^2 = 0.72$, $p < 0.001$; reptiles: $R^2 = 0.88$, $p < 0.001$; mammals: $R^2 = 0.54$, $p < 0.001$). Cross-taxon relationships between amphibians and reptiles indicated significant moderate associations for functional richness ($R^2 = 0.27$, $p < 0.001$), but also for Rao's quadratic entropy ($R^2 = 0.40$, $p < 0.001$). On the other hand, mammal functional diversity was significantly but weakly related with amphibian (functional richness: $R^2 = 0.09$, $p < 0.001$; Rao's quadratic entropy: $R^2 = 0.02$, $p < 0.001$) and reptile (functional richness: $R^2 = 0.13$, $p < 0.001$; Rao's quadratic entropy: $R^2 = 0.14$, $p < 0.001$) functional diversity (Figure 1d–f).

The climatic model performed better than the land–human model in all cases, and the overall model generally outperformed both the climate and land–human models (Table 1). In the case of functional richness, the explanatory power of the climatic model was (in descending order of fit): $R^2 = 0.59$ for reptiles, $R^2 = 0.42$ for amphibians, and $R^2 = 0.25$ for mammals. Meanwhile, the corresponding values of the land–human model were (in descending order of fit): $R^2 = 0.37$ for amphibians, $R^2 = 0.33$ for reptiles, and $R^2 = 0.10$ for mammals. The overall model including all the predictors was the best-fitting model in all cases, scoring slightly better than the climatic model. The highest explanatory power of the overall model was observed for reptiles, followed by amphibians and mammals, in all diversity metrics (Table 1, Figure 2), indicating that the variables related to landscape and human pressures play a subordinate role to climatic variables.

Table 1. Performance (R^2) of the generalized additive mixed models explaining the species richness, functional richness and Rao's quadratic entropy patterns of three taxonomic groups (amphibians, reptiles, and mammals) in Europe (grid cell size 50 km × 50 km). Temperature, precipitation, temperature seasonality, and precipitation seasonality were used to quantify the effects of climate in the climatic model, while land-cover diversity, agricultural land area, urban land area, and human population density were used to quantify the effects of land-cover and human pressures in the land–human model. All variables were used in the overall model.

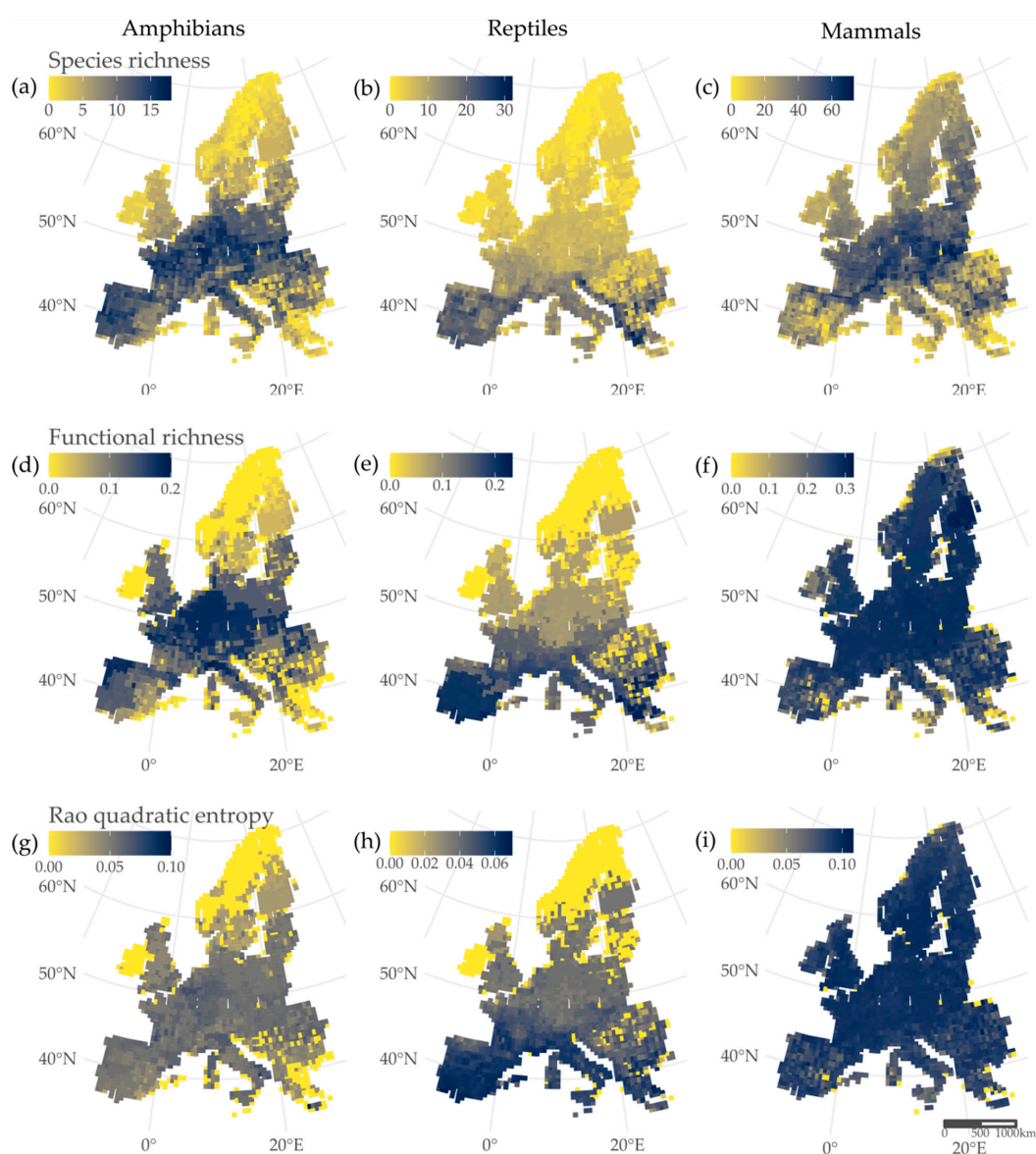| Diversity Aspect	Taxonomic Group	Climatic Model	Land–Human Model	Overall Model
Species richness				
	Amphibians	0.41	0.35	0.44
	Reptiles	0.60	0.34	0.65
	Mammals	0.30	0.19	0.35
Functional richness				
	Amphibians	0.42	0.37	0.47
	Reptiles	0.59	0.33	0.61
	Mammals	0.25	0.10	0.30
Rao's quadratic entropy				
	Amphibians	0.48	0.43	0.50
	Reptiles	0.61	0.38	0.61
	Mammals	0.23	0.10	0.27

Figure 1. The species richness (**a–c**), functional richness (**d–f**), and Rao's quadratic entropy (**g–i**) distribution patterns of amphibians, reptiles, and mammals in Europe (50 km × 50 km grid cell size).

The performance and shape of the relationship between the predictors (overall model) and each functional diversity metric and species richness for each taxon are summarized in Figure 2. Temperature and precipitation seasonality were significantly related to the species richness and functional diversity of all taxa. The species richness (as in the case of both indices of functional diversity) of amphibians and mammals had a unimodal relationship with temperature, while reptile species richness and functional diversity increased with it. Precipitation seasonality exhibited a convex relationship (suggesting the existence of a bimodal relationship, with the curve showing only a part of the variability) with diversity, independently of taxon or metric, although relatively little variation of their values was observed. Temperature seasonality significantly affected the species richness of all taxa, but only mammal and reptile functional richness was positively related to temperature seasonality. Reptile species and functional richness increased significantly with precipitation, and amphibians and mammals showed a unimodal relationship. A unimodal relationship was also found for Rao's quadratic entropy of mammals. Rao's quadratic entropy of amphibians decreased with increasing percentage of urban land area. All richness and diversity measures tended to have negative relationships with the

percentage of urban area. However, only in the case of reptile functional richness and Rao's quadratic entropy of amphibians was this negative relationship significant. Furthermore, the species and functional richness of amphibians and mammals tended to increase with the percentage of agricultural area, while a linear decreasing relationship was observed in the case of reptiles. Species richness for all taxa increased significantly with land-cover diversity. In addition, functional diversity measures tended to have a positive relationship with land-cover diversity, although these relationships were significant for reptiles, as well as for mammal functional richness. Finally, mammal species richness and amphibian Rao's quadratic entropy increased with human population density.
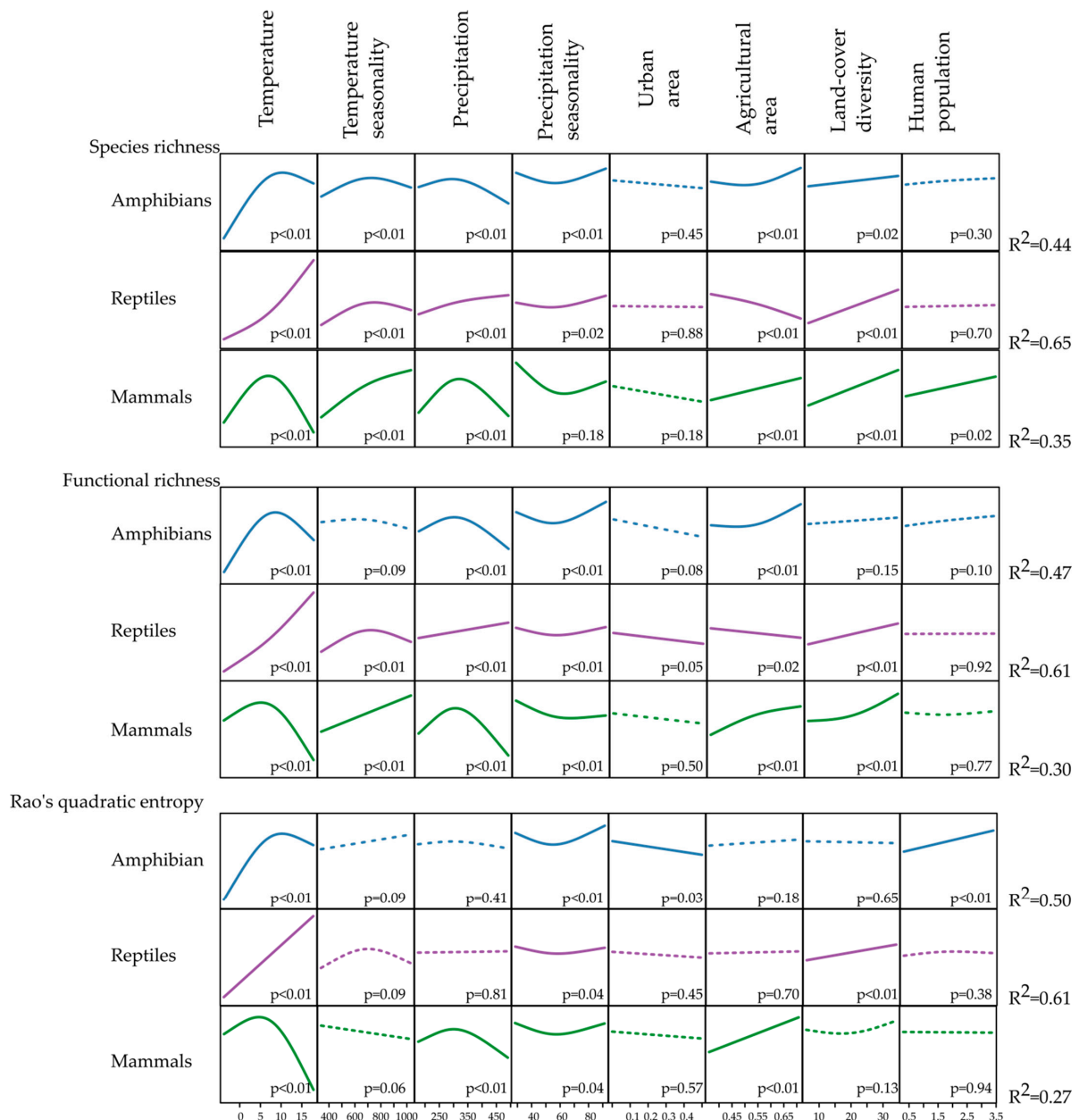

Figure 2. Summary plot showing the results of generalized additive mixed models (performance, direction, and significance of the relationship) predicting species richness, functional richness, and Rao's quadratic entropy of amphibian, reptiles, and mammals in Europe as function of climatic variables (temperature, precipitation, temperature seasonality, and precipitation seasonality) and variables related to land use and human pressures (land-cover diversity, agricultural land area, urban land area, and human population density). Continuous lines show significant associations while dotted lines show non-significant associations. Performance (R^2) is shown for the overall model in which all variables were used.

4. Discussion

4.1. Climatic Gradients

Climate overrides the effects of land use and human population density on shaping the functional diversity and species richness patterns of amphibians, reptiles, and mammals across Europe. The land–human model exhibited low explanatory power, but the land use variables and human population density slightly reinforced the explanatory power of the overall model in almost all cases (see the reptile Rao's quadratic entropy). Therefore, climate is the prevalent driver of functional diversity and species richness patterns [15,16], and although land use and human population density act at local scales [23,26], their imprint can be detected at broader scales [22].

Amphibian and reptile functional and taxonomic diversity varied along the climatic gradients, with different aspects of diversity within each taxon responding similarly to factors. The amphibian and reptile communities were species-poorer and functionally less diverse in Northern Europe, while reptile communities were species-richer and more diverse than amphibians in Southeastern Europe. The critical thermal minima of amphibians are lower than those of other ectothermic vertebrates, such as reptiles [44–46]. Therefore, the cooler temperatures of Northern Europe seem to exceed these thermal ranges and only a few species can survive there, which is reflected in their distribution [47] and functional diversity patterns [29]. In Southeastern Europe (e.g., along the coastline of the Mediterranean region), areas are characterized by high temperatures and moderate levels of precipitation, but higher seasonality. Amphibians and reptiles, as ectotherms, depend on the ambient temperature to thermoregulate, and other aspects of their physiology and behavior (e.g., reproduction) depend on the temperature and precipitation [48]. Amphibian distribution is associated more strongly with precipitation at the fine spatial scale [49]. Their body structure (i.e., the water permeability of their skin) is linked to thermoregulation, and the precipitation-dependent aspects of their ecology (e.g., most amphibians reproduce in the water) renders precipitation a crucial factor for their distribution [49,50]. Therefore, lower precipitation combined with higher temperatures (i.e., higher aridity) seems to restrict the number and range of the amphibian traits, resulting in higher trait similarity, and thus lower functional diversity [29]. In contrast, reptiles depend more strongly on temperature [49] and seem to be equipped with specific traits to cope well with high aridity [33].

Mammalian diversity patterns seem to tell a slightly different story. Their species richness varied along the climatic gradient, but mammalian functional diversity showed little variation and higher values compared to amphibians and reptiles across all of Europe. Some functionally homogeneous communities were detected scattered in Southern Europe but also in Northern Europe (particularly Norwegian coastal areas) and Ireland. The climatic and overall models performed less well for this taxon, implying that mammalian diversity is more weakly associated with climate compared to ectothermic taxa [49]. Furthermore, mammalian species richness is driven by environmental factors related to water–energy dynamics, for example, actual evapotranspiration and primary productivity in Europe [51] and globally [52], which were not included in the present study. On the other hand, functional diversity depends mostly on evolutionary time [52], and this perhaps is reflected in the lower predictive performance of our models. In temperate areas, the available time for niches to evolve, along with competition, energy availability, and adaptations to the environment, have resulted in functional divergence [19].

Seasonality was significantly related to the species richness and functional diversity of amphibians, reptiles, and mammals of Europe, confirming previous broad-scaled research on other taxa [14,16,19,29,53]. The species richness of ectothermic taxa had a unimodal relationship with temperature seasonality, while both species richness and functional diversity exhibited an approximately inverse unimodal relationship with precipitation seasonality. Amphibians are favored by low levels of precipitation seasonality that are observed in Central Europe, but also by high levels of precipitation seasonality that are observed in Southern Europe; however, in the latter region, temperature was a strong constraining

factor. Ochoa-Ochoa, Mejía-Domínguez, Velasco, Marske, and Rahbek [53] explored the amphibian functional diversity in America and reported a positive association between amphibian communities with precipitation and low precipitation seasonality, while temperature was not a significant driver. It is possible that precipitation seasonality acts together with temperature, resulting in functionally even amphibian communities in areas with low precipitation seasonality in Europe [29] and low to moderate temperatures. Low to moderate levels of temperature seasonality favored reptile species richness and functional diversity, while although the effect of precipitation seasonality was significant, reptile functional diversity varied little with it. Considering the positive strong effect of temperature on reptile communities and that temperature seasonality is higher at higher latitudes [54], climatic requirements were mirrored in the higher functional diversity in Southern Europe. At higher northern latitudes, reptile assemblages are more functionally constrained by seasonal changes, and the species pool consists of more similar traits [29]. Mammal species and functional richness increased with temperature seasonality and tended to decrease with precipitation seasonality, that is, Central Europe offers more suitable climatic conditions. Interestingly, the role of seasonality in mammals suggests either that species with a variety of trait values could co-occur regionally at higher latitudes [19] or that there is a potential discrimination between coastal and mountainous areas in Southern Europe associated with high temperature seasonality (dry/warm vs. cold/wet).

4.2. Anthropogenic Gradients

Beyond the prominent role of climate, land-use-related variables and human imprint emerged as weaker but significant determinants of the functional diversity and species richness of all examined taxa. Unsurprisingly, all taxa benefited from the land use diversity, as it reflects the habitat heterogeneity, that is, the availability of niches, which allows the coexistence of greater numbers of species with diverse functional traits [48,51]. Regarding human imprint, long-term human occupancy structures communities, with human pressures acting either as drivers or filters of functional diversity [24,25,33]. Amphibian (Rao's quadratic entropy) and reptile (functional richness) functional diversity decreased with the percentage of urban land area. Urbanization has a strong negative effect on amphibian and reptile assemblages, with few species having specific adaptations being able to secure their survival in urban areas [55], as in all fragmented and largely human-modified landscapes [11], and might result in the functional homogenization of communities [27]. Although amphibian functional diversity decreased with urban area, it increased with human population density, as has previously been shown for the species richness of different taxonomic groups [56,57]. Regarding the possible mechanisms for the positive richness, human population density invoking the suitability of climatic conditions, resource availability, and spatial heterogeneity [56] might explain the more functionally diverse amphibian communities in areas of higher human population density. On the other hand, agricultural area enhanced the richness (species and functional) of amphibians and disfavored reptiles. In a recent review [55], a non-significant, albeit negative, effect of agriculture on the species richness of these taxa was reported, but in the present study this was confirmed only for reptile functional diversity. Amphibians might benefit from the availability of water related to agriculture, or in some cases the matrix structure (e.g., possible landscape heterogeneity generated by the combination of agricultural and natural habitats) [55,58,59]. Inconsistent with recent research which reports that the trophic structure (an aspect of functional diversity) of communities highly exposed to human impacts is more simplified in terms of predicted structures with climate [60], here we found that mammalian richness and functional diversity were promoted by both the percentage of agricultural area and human population density. Low- to medium-intensity agriculture might conserve the diversity and functions of reptile communities [33,61], while the reported positive association between mammalian richness and human population density in Europe [56] seems to also apply to their functional diversity.

Although amphibians, reptiles, and mammals differ in their ecological roles, given the cross-taxon differentiations, these taxa shared some similarities in their responses and therefore in key functional roles [30]. Further investigation of mechanisms which drive functional diversity patterns considering data on different taxonomic groups could reveal further insights into how species functional roles can either complement or not respond to environmental variation. Climate, land uses, and other human-related factors influence species assemblages synergistically, making it difficult to decipher their individual effects on distribution patterns [33,62]; however, this might be related to the scale of the analysis. Here, we found that some human–landscape factors significantly affected diversity patterns at broad spatial scales. The consistency of the results was also extended to the different aspects of functional diversity (functional richness and Rao's quadratic entropy). Despite the acknowledged relationship between different functional diversity metrics [36,37], applying such analyses could help us to deepen our knowledge of how different aspects of functional diversity respond to environmental variation.

5. Conclusions

Our study highlighted the roles of climate and variables related to land uses and human pressures on shaping the species richness and functional diversity of amphibians, reptiles, and mammals in Europe. We found a strong effect of climate, with the role of human imprint being significant but of lower impact. The effect of urban land area and human population density on functional diversity patterns reported here might have irreversible negative impacts on taxonomic groups such as amphibians, thus resulting in the impaired provision of ecosystem services. However, our study highlights the importance of some human-related factors (e.g., agricultural area) that could preserve communities' functions under specific circumstances. In the era of global change, neglecting human imprint may lead us to misinterpret the effects of environmental variation on the distribution of species and traits [25]. Functional diversity, a significant dimension of biodiversity, bridges ecosystem functioning and community responses to environmental change [32]. Biodiversity hotspots for terrestrial vertebrates may be extensively influenced by climate change, especially in the Mediterranean bioregion [63]. Traditional conservation practices should also implement new approaches (e.g., including research on functional traits and functional diversity) to optimize conservation planning, and thus preserve ecosystem functioning. Enhancing our understanding of the determinants and processes that govern functional diversity patterns is valuable for maintaining ecosystem resilience and stability under the prism of climate and land use change.

Conflicts of Interest: The authors declare no conflict of interest.

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