Climate–diversity relationships underlying cross-taxon diversity of the African fauna and their implications for conservation

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Abstract

Aim: Many taxa show remarkable similarities in their diversity patterns, and these similarities are commonly used to define large-scale conservation priorities. Here, we investigated the relative importance of contemporary climate and climate change since the Last Glacial Maximum for determining the species richness and rarity patterns of four animal taxa. We assessed the extent to which diversity patterns are congruent across taxa because of similar responses to these climatic aspects, and we identify regions that are disproportionately diverse due to their palaeoclimatic stability.

Location: Sub-Saharan Africa.

Time period: LGM–contemporary.

Major taxa studied: Mammal, bird, amphibian and dragonfly species.

Methods: Diversity patterns were predicted based on their relationships with contemporary climate and Quaternary climate change, respectively. Climate–diversity relationships were modelled with and without accounting for spatial autocorrelation. For raw and predicted diversity patterns, cross-taxon congruence and the coverage of diversity hotspots by protected areas were determined.

Results: Species richness and rarity of all taxa increased with increasing temperature and precipitation, but also with increasing palaeoclimatic stability. Cross-taxon congruence was higher for predictions based on contemporary climate than for predictions based on Quaternary climate change. Protected areas covered 17%–37% of the species richness and rarity hotspots and approximately 6% fewer hotspots of the underlying signatures of Quaternary climate change (i.e. biodiversity refugia).

Main conclusions: Both contemporary climate and past climatic changes strongly affect species richness and rarity patterns. However, whereas contemporary climate–diversity relationships are largely congruent across taxa, signatures of Quaternary climate change differ among taxa. Furthermore, protected areas emphasize regions with high species richness and rarity but fewer biodiversity refugia—even less than expected by random placement (<21%). Our results highlight the importance of historical factors for shaping large-scale diversity patterns and the potential of using...
1 | INTRODUCTION

The continuing loss of biodiversity across the globe (Hof, Araújo, Jetz, & Rahbek, 2011; Parmesan & Yohe, 2003; Scheffers et al., 2016) has led to numerous calls for more effective conservation strategies (e.g. Rodrigues & Brooks, 2007; Vane-Wright, Humphries, & Williams, 1991). As data on species’ distribution ranges are generally readily available, large-scale conservation strategies largely focus on regions containing many species as well as high concentrations of rare species (Darwall et al., 2011; Grenyer et al., 2006; Margules & Pressey, 2000; Prendergast, Quinn, Lawton, Eversham, & Gibbons, 1993). However, species richness and rarity poorly account for the influence of historical factors for shaping diversity patterns of taxa and strategies focusing on these diversity measures may therefore miss areas of high importance for conservation (e.g. Fritz & Rahbek, 2012; Hortal et al., 2011; Jetz, Rahbek, & Colwell, 2004). Thus, the strong effects of contemporary climate on patterns in species richness and rarity likely hamper inferences of regions where, for instance, climatic stability favoured the survival of species during the late Quaternary. Identifying such climate-induced biodiversity refugia increased in priority for conservation planning, because biogeographically unique (relict) species have persisted therein during past climatic changes, but also because past and anticipated future climatic changes are highly correlated (Sandell et al., 2011) whereby species will likely retreat to such regions in the future (Taberlet & Cheddadi, 2002; reviewed in Keppel et al., 2012).

Determinants of biodiversity patterns can be broadly divided into contemporary and historical factors (Wiens & Donoghue, 2004). By far the most general pattern of biodiversity is a decrease in species richness from the equator to the poles along with decreasing temperature and precipitation (contemporary climate hypothesis; Hawkins et al., 2003; Waide et al., 1999). Therefore, similar responses of taxa to contemporary climate are considered the main reason for congruent species richness patterns across taxa (Grenyer et al., 2006; Orme et al., 2005; Prendergast et al., 1993). Nevertheless, the statistically strong relationships between the species richness of taxa and contemporary climate often leave much of the variation in species richness unexplained (typically between 10% and 60%; Hawkins et al., 2003; Hillebrand, 2004; Waide et al., 1999) and this unexplained variation has been shown to mainly reflect the impact of historical factors on biodiversity patterns. Thus, assemblages with a higher richness than predicted by contemporary climate tend to cluster in regions where many phylogenetically or biogeographically unique species occur (Jetz et al., 2004; McGlone, 1996; Pinkert et al., 2018; Rahbek et al., 2019).

In addition to regions with a high species richness, those with many rare species are frequently targeted as conservation priorities, as they are assumed to exemplify the impact of historical factors on species distributions (e.g. Lamoreux et al., 2006) and because rare species are particularly vulnerable to extinction (Lee & Jetz, 2008; Ricketts, 2001). However, the use of geographical rarity patterns as a surrogate for the signature of historical factors is also known to suffer from the direct effect of contemporary climate on rarity and its indirect effect via the relationships between species richness and rarity. For example, it is well-documented that warmer regions and regions with a lower climate seasonality contain more rare species (more species with small range sizes) than colder regions and regions with a higher climate seasonality (Rapport, 1975; see also Baselga, 2008; Schultd & Assmann, 2009). In addition, patterns of species richness and rarity can be inherently correlated, as regions with many species will also by chance contain a larger number of rare species (Jetz et al., 2004). Thus, strong relationships of both species richness and rarity with the contemporary climate may obscure differences in the response of taxa to historical factors and potentially mislead conclusions about climate-induced refugia for biodiversity (the signature of relict species).

An important factor shaping current diversity patterns of many taxa can be strong palaeoclimatic disturbance events (e.g. glaciations) that made certain regions inhabitable for most species over thousands of years, whereas the palaeoclimatic stability in other regions favoured the persistence of species (historical climate stability hypothesis: Currie, 1991; Davies, Purvis, & Gittleman, 2009; Jetz et al., 2004; Kerr & Currie, 1999). For instance, regions south of the zero-degree isotherm of the Last Glacial Maximum in Europe and North America often have a higher species richness as well as higher numbers of rare species or lineages than previously glaciated regions (Araújo et al., 2008; Castro-Insua, Gómez-Rodríguez, & Baseiga, 2016; Pinkert et al., 2018). These patterns indicate that most species, and particularly rare species and lineages, are still confined to southern glacial refugia. However, current knowledge about potential biodiversity refugia is strongly biased towards Holarctic regions, where many species are limited by their thermal tolerance and where the availability of detailed fossil and genetic information facilitated palaeobiological and phylogeographical inferences of refugia (reviewed in Keppel et al., 2012). Thus, tolerance limits of general importance for ecologically diverse taxa such as the 0°C isotherm

**Keywords**

biodiversity refugia, climate stability during the late Quaternary, cross-taxon congruence, geographical range size, palaeoecology, priority areas for conservation, the signature of historical factors underlying diversity patterns.
might be not globally relevant and a focus on regions moulded by glaciers likely simplifies the overall complexity of species’ responses to climatic changes (deep time/ historical/ millennial/ annual fluctuations in temperature or precipitation). For instance, it is increasingly recognized that refugia in unglaciated regions are associated with more mesic conditions compared to surrounding regions (Bowler, Wyrwoll, & Lu, 2001; Hemp, Scherer, Brandl, & Pinkert, 2020; Nichol, 1999). However, some of these mesic refugia may not even exist long enough to provide a palaeoecological record or signals in the phyleogeography of taxa. Thus, inferences of biodiversity refugia are not only biased towards North America and Europe, but also to temperature and particularly glacial refugia (reviewed in Keppel et al., 2012). Consequently, we still largely lack a general understanding of the ecological processes that define refugia and the extent to which refugia are similar among ecologically different [e.g. terrestrial and (semi)aquatic] taxa. Given the role of biodiversity refugia for the survival of relict species and as safe havens for biota under future climatic changes, such an understanding would be, however, of major importance of guiding global conservation prioritization.

In this study, we assess the relative importance of contemporary climate and climatic changes since the Last Glacial Maximum (LGM) for shaping species richness and rarity patterns of mammals, birds, amphibians and dragonflies across sub-Saharan Africa. Specifically, according to the contemporary climate hypothesis, we expect that (1) the species richness and rarity of the considered taxa strongly and similarly increase with increasing temperature and/or water availability. Furthermore, in line with the climate stability hypothesis, we predict that (2) species richness and rarity are generally higher in regions with a high climate stability during the Quaternary. However, we hypothesize that terrestrial taxa respond stronger to temperature changes whereas semiaquatic taxa respond stronger to precipitation changes since the LGM and, therefore, expect that the responses of taxa to Quaternary climatic changes will be more different than their (raw) species richness and rarity patterns. Hence cross-taxon congruence of biodiversity refugia should be lower. We thereby aim to understand the generality of response to climatic stability during the Quaternary and their potential for identifying past and future refugia at large spatial and taxonomic scales. Finally, given the common focus on hotspots of species richness and rarity in conversation planning, we test whether (3) potential biodiversity refugia are less covered by established protected areas than hotspots of raw species richness and rarity as well as than expected by chance.

2 | METHODS

2.1 | Distribution data

Our analyses were based on vector maps of the distributions of all 1,001 terrestrial mammalian species, 1,942 bird species and 723 amphibian species (from IUCN, 2016 and BirdLife International and NatureServe, 2015) as well as all 731 dragonfly species (from Clausnitzer et al., 2012, accessed August 16, 2016) of sub-Saharan Africa. We limited our study to this coherent biogeographical region (south of 17.5°N latitude) to avoid a misestimation of the rarity of those North African species which ranges extend to parts of Europe and Asia. Furthermore, Madagascar and smaller islands were excluded to avoid the effects of low sample size and incomplete sampling (see e.g. Pinkert, Brandl, & Zeuss, 2017). Vector maps were reassigned to a grid with a grain size of approximately 50 km × 50 km (Lambert azimuthal equal area projection centred on 5°N 20°E) using functions provided in the R-package raster (Hijmans et al., 2016). This grain size was chosen because it offered a compromise between data quality (particularly relevant for the palaeoclimatic data) and overestimation of the distributions of those species with very limited ranges (Hurlbert & Jetz, 2007). Spatial data were imported and converted using the R-packages raster and rgdal (Bivand, Keitt, et al., 2017; Hijmans et al., 2016). Colour scale intervals in the cartographical illustrations were classified using functions of the R-package classInt (Bivand, Ono, Dunlap, & Stigler, 2017).

2.2 | Overall diversity patterns and their hotspots

Based on the distribution data, we first calculated the species richness and rarity of the assemblages. Subsequently, we predicted the variation in these diversity patterns based on contemporary climate and the climatic changes since the LGM, respectively (see the section “Statistical analysis,” below). Hotspots of diversity patterns were arbitrarily defined as the 300 grid cells with the highest (raw or predicted) species richness and rarity. Following Orme et al. (2005), we evaluated the influence of this definition by calculating the overlap between taxa for the top 1–2,000 grid cells with the highest species richness and rarity, respectively.

Endemism is commonly defined as the proportion of species restricted to a particular area (Williams, 2000). According to this definition, almost all the herein considered mammalian, bird, amphibian and dragonfly species are endemic to sub-Saharan Africa. Nevertheless, many of these species are widespread across the study region. To distinguish between areas with a large proportion of widespread species and those with a large proportion of rare species, we used the corrected weighted endemism of species assemblages, that is the geometric mean of the inverse occupancy of species in a grid cell, instead of endemism sensu stricto (Williams, 2000). Corrected weighted endemism emphasizes species with relatively small ranges. For example, a species occurring in only one grid cell has the weight 1(1/1), whereas a species occurring in two grid cells has the weight 0.5(1/2). We used this common measure of rarity rather than, for instance, measures of relative rarity (e.g. patterns of the 25% species with smallest ranges; Leroy, Canard, & Ysnel, 2013), to facilitate the comparison with species richness patterns of the taxa and comparisons with previous studies on large-scale rarity patterns. It is, however, worth noting that further parametrization might be necessary if cross-taxon congruence is low or if rarity–occupancy curves differ in their form among taxa (Leroy, Gallon, Feunteun, Robuchon, & Ysnel, 2017; but see Figure S1).
2.3 | Environmental data

We evaluated the importance of contemporary climate and climatic changes since the LGM (PMIP boundary conditions for the LGM, CCSM4 coupled climate model prediction) for shaping the species richness and rarity patterns of the considered taxa, based on the same 19 bioclimatic variables for each time period. The environmental variables were downloaded from http://chelsa-climate.org (Karger et al., 2017, 2018). All variables were aggregated to obtain mean values for the grid cells. Although topography can be an important driver of rarity and might therefore shape biodiversity patterns, this aspect of the environmental setting was not considered in the analysis because there has been very little change in the topography of Africa during the last 21,000 years.

Summarizing all 11 temperature and all 8 precipitation variables into two principal components, each, based on a correlation matrix with the functions provided in the R-package stats, indicated high contributions of annual mean temperature (AMT), temperature seasonality (TS), annual precipitation (AP) and precipitation seasonality (PS) to the overall trends in temperature and precipitation, respectively (for variable loadings, see Table S1). The results obtained for models of these selected variables are similar to those based on principal components (differences between the scores predicted based on eigenvectors from the principal component analysis of contemporary climate; Table S2). To facilitate an interpretation of the results and the comparison with previous studies (e.g. Araújo et al., 2008), we therefore focused on these four variables for assessing the effects of contemporary climate and climatic changes since the LGM on patterns of species richness and rarity. To estimate climatic changes since the LGM, for each grid the AMT, TS, AP and PS values during the LGM were subtracted from those of the corresponding contemporary climate variables (ΔAMT, ΔTS, ΔAP, ΔPS; see also Araújo et al., 2008). The main advantage of using these differences describing climatic changes since the LGM as predictors was that, in contrast to the LGM climate variables themselves, they are largely independent of contemporary climate (AMT vs. ΔAMT: p < .001, R² = .08; TS vs. ΔTS: p < .001, R² = .30; AP vs. ΔAP: p < .001, R² = .07, PS vs. ΔPS: p < .001, R² = .02; also see Figure S2).

To evaluate the robustness of the results to the choice of gain size, we repeated the analyses based on a 100 km × 100 km resolution. Because the results obtained for models of the selected environmental variables at a resolution of 50 km × 50 km were similar to those of models based on this resolution (Table S3), we focused on the former for facilitating applied nature conservation.

2.4 | Statistical analyses

2.4.1 | Effects of contemporary climate and palaeoclimatic change on diversity patterns

To assess the relative importance contemporary climate and Quaternary climate change for shaping species richness and rarity and to separate their effects, we fitted two sets of models using simple ordinary least squares regressions. In the first set of models, the species richness and rarity of the assemblages were dependent variables and contemporary climate variables were predictors. In the second, the species richness and rarity of the assemblages were dependent variables and variables describing Quaternary climate change were predictors. However, spatial correlograms indicated significant spatial autocorrelation in the model residuals, with spatial independence reached at distances between 400 km and 1,500 km, dependent on which diversity measure was considered (Figure S3). Because such spatial autocorrelation structures may lead to an overestimation of the effective degrees of freedom (Dormann, 2007), we repeated the analyses using spatial simultaneous autoregressive error models implemented in the R-package spdep (Bivand, Altman, et al., 2017). This method allowed an assessment of the spatially corrected p-values of the models by fitting a spatial weight based on a neighbourhood matrix (great circle distances of neighbouring grid cells) with the specific points of spatial independence (Figure S3) representing the maximum boundaries of the matrix.

Based on these models, we then predicted the variations in species richness and rarity explained by contemporary climate and Quaternary climate change, respectively, using the function predict.sarlm of the R-package spdep (fit component, TS prediction type; Bivand, Altman, et al., 2017). To facilitate comparisons of effect sizes between models, all predictor variables were z-standardized using functions of the R-package base. Note that whereas in other studies the residuals of contemporary climate–diversity relationships have been interpreted (e.g. Rahbek et al., 2019), we here used the predictions based on Quaternary climate change to separately compare and map the signature of palaeoclimatic stability underlying diversity patterns of the considered taxa (i.e. biodiversity refugia). With a supplementary analysis, we confirmed that Quaternary climate change accounts for a large part of the variation in species richness and rarity that is left unexplained by contemporary climate (Figure S4) and that hotspots of the signature of Quaternary climate changes contain more narrow-ranging species than regions outside these hotspots (Figure S5). As regional range size, local range size and local abundance are inherently correlated (Pinkert et al., 2020), these hotspots likely reflect species that are particularly rare and vulnerable to extinction. We used the predicted part of variation in species richness and rarity based on Quaternary climatic changes instead of interpreting the residuals of contemporary climate–diversity relationships themselves or using the LGM climatic variables as predictors of the signature of historical factors to avoid two methodical issues. First, although the set of contemporary environmental variables included in our models explained a substantial part of the variation in the diversity patterns of the taxa, an analysis of the residuals of these relationships may be sensitive to the selection of predictor variables and measurement errors therein as well as sampling bias in the distribution data (e.g. Herkt, Skidmore, & Fahr, 2017). Second,
Table 1 Standardized coefficients (z-scores) of predictors from multiple regressions (OLS: ordinary least squares and SAR: spatial simultaneous autoregressive error models) between the overall species richness and rarity patterns of four animal taxa and contemporary climate as well as Quaternary climate change (contemporary minus LGM climate) across sub-Saharan Africa (6,635 grid cells of 2,500 km² size). In addition, total explained variance (i.e. $R^2$ for OLS and Nagelkerke pseudo-$R^2$ for SAR) are presented. Variables: AMT, annual mean temperature; TS, temperature seasonality; AP, annual precipitation; PS, precipitation seasonality as well as their changes since the LGM ($\Delta$). Only effects that were significant at $p < .05$ are shown and all effects were multiplied by 100 for reasons of clarity.

| Div.  | Model | Taxon    | Contemporary climate | Quaternary climate change |
|------|-------|----------|----------------------|--------------------------|
|      |       |          | AMT  | TS   | AP   | PS    | $R^2$ | $\Delta$AMT | $\Delta$TS | $\Delta$AP | $\Delta$PS | $R^2$ |
| Richness | OLS  | Mammals  | -12  | -21  | +23  | -3.0  | .47  | -30         | -24         | +12       | +10       | .13  |
|         |      | Birds    | -32  | -41  | +16  | +1.1  | .37  | -33         | -29         | +6.2      | +5.0      | .17  |
|         |      | Amphibians | -22 | -73  | +69  | +11.1 | .53  | -37         | -31         | +6.4      | +31       | .22  |
|         |      | Dragonflies | -11 | -24  | +59  | -7.7  | .73  | -46         | -35         | +14       | +27       | .31  |
|         | SAR  | Mammals  | -14  | -23  | +12  | -3.1  | .67  | -9.4        | -15         | +3.7      | .54  |
|         |      | Birds    | -26  | -45  | +13  | -9.6  | .61  | -17         | -18         | +9.4      | -9.7      | .47  |
|         |      | Amphibians | -10 | -24  | +45  | -4.2  | .69  | -13         | -19         | +4.4      | .52  |
|         |      | Dragonflies | -28 | +36  | -1.5 | .83  |     | -19         | -19         | +2.7      | -3.8      | .66  |
| Rarity | OLS  | Mammals  | -14  | +8.0 | +6.4 | -56   | .41  | -29         | -5.4        | -22       | .14  |
|         |      | Birds    | -28  | -23  | -18  | -50   | .48  | -30         | -8.8        | -18       | -19       | .19  |
|         |      | Amphibians | -20 | -12  | -20  | -20   | .49  | -23         | -10         | -15       | -3.8†     | .09  |
|         |      | Dragonflies | -16 | -72  | +60  | -16   | .69  | -43         | -29         | +6.1      | +22       | .23  |
|         | SAR  | Mammals  | -23  | +13  | -46  | .59  |     | -18         | -16         | -25       | .38  |
|         |      | Birds    | -34  | -22  | -36  | .64  |     | -15         | -17         | -15       | -15       | .44  |
|         |      | Amphibians | -23 | -18  | +5.0 | -17   | .61  | -23         | -21         | -15       | .20  |
|         |      | Dragonflies | -1.5| -8.9 | +36  | -31   | .78  | -19         | -21         | -4.0      | .49  |
because the contemporary and LGM climate are inherently related (Figure S2), it is difficult to separate their contributions for shaping species distributions. We are convinced that this approach currently represents the best possible solution to separately compare and map the contribution of palaeoclimate for shaping diversity patterns.

### 2.4.2 Drivers of cross-taxon diversity

Congruence in the overall patterns of the raw species richness and rarity as well as of predictions based on climate–diversity relationships was quantified as the coefficient of determination from pairwise correlations of the diversity patterns ($r^2$). We did not use a spatially corrected measure of congruence, because the spatial autocorrelation structure underlying the compared diversity patterns was similar (Figure S3) and to be able to compare these patterns later with the spatially clustered distribution of established protected areas. In addition, the degree of overlap between hotspots of these diversity patterns across the considered taxa and the coverage of the hotspots by protected areas was determined. Congruence tables of diversity patterns were generated using the R-package corrplot (Wei & Simko, 2014).

### 2.5 The current protection status of diversity hotspots

To assess the coverage of diversity hotspots by established protected areas, spatial polygons of the protected areas of the world were downloaded from Protectedplanet.net (UNEP-WCMC 2016 and IUCN 2016, accessed May 21, 2016). For our analysis, we used all established non-marine protected areas of sub-Saharan Africa (categories Ia, Ib, II, III, IV, V and VI). However, by also including areas designed to protect cultural landscapes, natural monuments or gaming reserves (categories III to VI), our broad definition of protection probably overestimated the actual coverage of biodiversity hotspots by protected areas. Hence, our analysis of protected areas is an overestimation of the protection status of the biodiversity of sub-Saharan Africa. Functions of the R-package raster (Hijmans et al., 2016) were used to intersect protected area shapes with our grid. The size of these intersections (in km$^2$) was then divided by the total size of each grid cell (2,500 km$^2$) to obtain the relative coverage of each of the 6,635 cells by protected areas. Since very small fragments of protected areas would result in an overestimation of the actual coverage of diversity hotspots, calculations of the coverage of diversity hotspots were repeated for cells that intersected with the protected areas by $>$5%, $>$10% and $>$20% of their area. To compare the observed hotspot coverage with the coverage that is expected by chance, we randomized the locations of the protected areas 1,000 times and averaged coverage of the identified diversity hotspots.

### 3 RESULTS

#### 3.1 Effects of contemporary climate and Quaternary climatic change on diversity patterns

In ordinary least squares regressions, contemporary climate explained more, or at least as much, of the variance in the diversity patterns of the taxa (species richness: $0.61 < r^2 < 0.87$; rarity: $0.61 < r^2 < 0.78$) as did Quaternary climate change (species richness: $0.47 < r^2 < 0.66$; rarity: $0.20 < r^2 < 0.49$; Table 1; for single regressions, see Figures S6 and S7). Both species richness and rarity generally decreased with increasing annual mean temperature, temperature seasonality and precipitation seasonality and increased with annual precipitation (except for rarity patterns of birds and amphibians, Table 1). In addition, species richness and rarity generally decreased with increasing changes in temperature and precipitation during the last 21,000 years.

#### 3.2 Drivers of cross-taxon congruence

The patterns for raw species richness and rarity across all taxa were largely congruent (defined as $r^2 > 0.25$; Figures 1 and 2). In predictions of species richness and rarity based on contemporary climate, cross-taxon congruence strongly increased ($r^2$ increased by $0.22$ on average; see Figure 2 and, for the differences, Figure S8), whereas in predictions based on Quaternary climate change, it strongly decreased ($r^2$ decreased by $0.14$ on average).

#### 3.3 Hotspots of cross-taxonomic diversity

The congruence of species richness and rarity hotspots across the four considered taxa was lower than the congruence among the overall diversity patterns. Only hotspots of the species richness and rarity of birds and mammals as well as hotspots of the rarity of mammals and dragonflies had a high percentage of overlap (defined as more than 50%; Figures 1 and 2). These results were robust for different definitions of hotspots, that is, the relative proportion of overlap across taxa (congruence) remained similar when increasing the number of top-ranked grid cells considered in the calculations (Figure S9). The degree of overlap of diversity hotspots was similar for predictions based on contemporary climate and those based on raw diversity patterns (1% decrease in overlap), but decreased for predictions based on Quaternary climate change (7% decrease in overlap, see Figure 2; for the differences see, Figure S8).

#### 3.4 The current protection status of diversity hotspots

According to the broadest definition of coverage by protected areas, 1,312 of the 6,635 cells overlapped with protected areas of any IUCN
category for more than 5% of their area. If only cells with >10% and >20% overlap were considered, the coverage of hotspots by protected areas decreased considerably, but the ranking of coverage among taxa remained similar (Table 2). For the broadest definition of coverage, protected areas covered 17%–37% of the hotspots of species richness and rarity, and 9%–35% of the hotspots predicted based on Quaternary climate change. The coverage of hotspots by protected areas was approximately 10% higher for mammals and birds than for amphibians and dragonflies. Randomizing the locations of protected areas showed that many biodiversity refugia and rarity hotspots, particularly those of freshwater taxa, are even less well covered by protected areas than expected by chance (approximately 21%).

4 | DISCUSSION

Our results highlight that both contemporary climate and climatic changes during the Quaternary strongly shaped the diversity patterns of African mammals, birds, amphibians and dragonflies. Species richness and rarity of all taxa increased with increasing temperature and precipitation, but also with increasing climatic stability during the Quaternary. Whereas the overall diversity patterns of the considered taxa, and, albeit to a much lower degree, hotspots of diversity were congruent mainly because of similar responses to contemporary climate, the relative importance of changes in temperature and precipitation since the LGM differed among taxa. Furthermore, our results showed that assemblages in regions with a high climatic stability during the Quaternary are disproportionally diverse (i.e. contain more species and more rare species than expected from models based on contemporary climate) and that these biodiversity refugia are rather poorly covered by protected areas.

4.1 | The importance of past climatic changes for shaping species’ distributions

While the distributions of species, in addition to contemporary climate, are partly influenced by many ecological and evolutionary processes, such as biotic interactions (e.g. Dormann et al., 2018), evolutionary constraints (e.g. Safi et al., 2011) and anthropogenic influences (e.g. Faurby & Svenning, 2015), our results clearly indicate that Quaternary climate change is a major driver of patterns in the species richness and rarity of mammals, birds, amphibians and dragonflies across sub-Saharan Africa (Table 1). The signature of Quaternary climate change underlying diversity patterns highlighted regions characterized by lower changes in annual mean temperature and annual precipitation during the last 21,000 years. Such climate-induced
biodiversity refugia are, for instance, the Albertine Rift, equatorial Africa, the Horn of Africa and the Cape region (Figure 3). Together with previous studies on the range size of mammals (Davies et al., 2009) as well as plants (Harrison & Noss, 2017) and the species richness of European amphibians (Araújo et al., 2008), our results indicate that climatic changes since the LGM have consistently left a strong imprint on the diversity patterns of many taxa. Moreover, in line with Rahbek et al. (2019) who postulated that mountainous regions of the world harbour a higher richness of vertebrate species than expected from models based on area and contemporary climate due to their function as biodiversity refugia, we showed that the species richness and rarity of African mammals, birds, amphibians and dragonflies are disproportionately higher in regions with a higher climatic stability during the Quaternary. Latter regions were mostly, but not exclusively, mountainous regions, which suggests that an understanding of the effects of climate stability during the Quaternary on speciation and extinction dynamics might represent a more general approach for the identification of biodiversity refugia (c.f. Rahbek et al., 2019).

Despite the overall importance of climatic stability during the Quaternary, the relative importance of changes in temperature and precipitation during the last 21,000 years differed among taxa. Specifically, neither the species richness of mammals and amphibians nor the rarity of mammals, amphibians and dragonflies was influenced by changes in precipitation seasonality (Table 1). The most remarkable contradiction of the climate stability hypothesis was, however, a strong increase in the species richness of all considered taxa with increasing changes in annual precipitation since
the LGM, which has resulted in a greater diversity than expected based on models of contemporary climate in semi-arid regions of sub-Saharan Africa. This pattern cannot be explained by the admixture of species from deserts and tropical rain forests, because the effects of climatic changes since the LGM were essentially independent from those of contemporary climate. Instead, the relatively high diversity may be the result of species whose distributions during the last 21,000 years underwent contraction when continuous tropical forests converted to savannas (Kröpelin et al., 2008). Whereas the climatic changes since the LGM are

| Model            | Taxon  | Species richness | Rarity |
|------------------|--------|------------------|--------|
|                  |        | >5% | >10% | >20% | >5% | >10% | >20% |
| Raw              | Mammals | 0.37 | 0.31 | 0.24 | 0.24 | 0.20 | 0.15 |
|                  | Birds   | 0.37 | 0.31 | 0.22 | 0.30 | 0.26 | 0.18 |
|                  | Amphibians | 0.29 | 0.23 | 0.17 | 0.18 | 0.15 | 0.10 |
|                  | Dragonflies | 0.19 | 0.15 | 0.13 | 0.17 | 0.13 | 0.09 |
| Biodiversity refugia | Mammals | 0.35 | 0.32 | 0.27 | 0.16 | 0.14 | 0.11 |
|                  | Birds   | 0.35 | 0.30 | 0.25 | 0.16 | 0.14 | 0.11 |
|                  | Amphibians | 0.21 | 0.18 | 0.15 | 0.16 | 0.14 | 0.10 |
|                  | Dragonflies | 0.13 | 0.12 | 0.10 | 0.09 | 0.08 | 0.07 |

**FIGURE 3** Overlap of the hotspots of the raw diversity patterns (species richness and rarity) of four animal taxa and of predictions based on spatial autoregressive error models of the relationships between diversity patterns Quaternary climate change (contemporary minus LGM climate; i.e. potential biodiversity refugia) across sub-Saharan Africa (6,635 grid cells; Lambert azimuthal equal area projection). Hotspot areas are defined as the top 300 grid cells of each aspect of diversity. The colour scale indicates the number of taxa with overlapping hotspots and whether these hotspots are protected or not (i.e. whether established protected areas cover >5% of the area of a cell)

**TABLE 2** Coverage of diversity hotspots of four animal taxa by protected areas for raw species richness and rarity patterns and for predictions based on spatial autoregressive error models of the relationships of species richness and rarity with the Quaternary climate change (contemporary minus LGM climate) across sub-Saharan Africa (6,635 grid cells of 2,500 km² size). In addition, results for three different overlap definitions (area of coverage of a grid cell by protected areas of any IUCN category) are provided: >5% (1,312 cells), 10% (1,134 cells) or >20% coverage (909 cells). Hotspots are defined as the 300 grid cells with the highest number of species and density of endemic species as well as the highest species richness and density of endemic species predicted based on Quaternary climate change–diversity relationships (i.e. potential biodiversity refugia)
presumably the most important historical factor shaping contemporary species distribution, it can be safely assumed that, at evolutionary time scales, all extant species passed through the climate change extinction filters several times (Davies et al., 2009). Hence, the effects of climatic stability during the Quaternary on biodiversity patterns are likely to, not only reflect past extinctions, but also long-term evolutionary dynamics. Therefore, our results suggest that high climatic changes might have favoured the diversification of a few lineages bearing adaptations (e.g. drought tolerance and diapause) that allowed them to persist in or (re-)colonize less stable habitats and regions (Araújo et al., 2008; Pinkert et al., 2018). Thus, although comprehensive phylogenies for most taxa are lacking, understanding similarities in the relationships between past climatic changes and phylogenetic diversity patterns offers an interesting avenue for future investigations.

### 4.2 Implications for setting large-scale conservation priorities

Besides macroecological studies increasingly recognize the importance of historical factors for shaping large-scale diversity patterns of taxa and although conservation planning is fundamentally based on hotspots of species richness and rarity of different taxa, we argue that considering the impact of climate–diversity relationships at management-relevant scales, such as hotspots, has important implications for strategic conservation planning:

First, our results highlight that the contemporary climate is consistently the main driver of not only species richness, but also of rarity patterns of ecologically very different taxa (ectotherms vs. endotherms, terrestrial vs. freshwater species, vertebrates vs. invertebrates). Furthermore, congruence of overall species richness and rarity patterns of the same taxon was mainly driven by responses to contemporary climate (congruence: 44.5% on average compared to 28.5% for responses to climate change since the LGM; Figure 2). These results suggest that biogeographical inferences and assessments of conservation priorities based on rarity patterns can lead to misinterpretations of the signature of climate stability during the Quaternary underlying diversity patterns if they do not account for confounding effects of species richness as well as geometric and climatic constraints (see also Jetz et al., 2004; Rahbek et al., 2019).

Second, our results indicate that although the overall diversity patterns are basically congruent, the signature of climatic changes during the Quaternary underlying diversity patterns differed among taxa and that the hotspots of these signatures are rather poorly covered by established protected areas. According to the most optimistic definition of protection (5% coverage by protected areas of any IUCN category), established protected areas cover a considerable proportion of sub-Saharan Africa. However, these areas comprise a relatively small proportion of hotspots of species richness and rarity (17%–37%) and an even smaller proportion of hotspots of the signature of Quaternary climate change underlying species richness and rarity patterns (9%–35%, Table 2). In this respect, it is important to stress that, due to the high coverage of sub-Saharan Africa by established protected areas, even a random placement of protected areas results in approximately 21% coverage (average across 1,000 randomizations; c.f. Olivo et al., 2016). Our study shows that due to a greater climatic stability during the Quaternary a disproportionately high diversity is found at the Horn of Africa, the Cape region and equatorial Africa. We are convinced that although these hotspots are partly similar to the hotspots of raw species richness and rarity (mammals: 9%, birds: 18%, amphibians: 48%, dragonflies: 25%) and although they are presumably known by specialist, the mapping of potential refugia may serve as a baseline for setting complementary conservation foci as well as for further local-scale assessments of the faunas in these regions.

Third, our results revealed that current conservation strategies emphasize hotspots of well-known terrestrial taxa, with coverage by established protected areas being approximately 10% lower for hotspots of dragonflies and amphibians than for mammals and birds. This taxonomic bias in current conservation strategies is especially relevant because recent population trends of freshwater taxa indicate a severe and global crisis in freshwater systems, particularly in tropical streams (Dudgeon et al., 2006; Hof et al., 2011). In fact, the combination and interaction of different threats are estimated to lead to an extinction risk that is three times higher for freshwater species than for any terrestrial taxon (IUCN Red List of Threatened Species 2018).

Finally, with 4.66°C on average, changes in annual mean temperature across sub-Saharan Africa since the LGM are already comparable to the magnitude of anticipated anthropogenic changes in global temperatures until the year 2,100 (most likely 2–3°C on average; IPCC, 2014). Depending on the considered regions, absolute changes in temperature since the LGM ranged from 0.46°C to 9.46°C and our results highlight that mammalian, bird, amphibian and dragonfly assemblages in climatically stable regions had consistently a higher species richness and rarity species than those in climatically less stable regions. Thus, some regions remained remarkably stable in their climate during the last 21,000 years and still contain many relict species. Therefore, focusing conservation priorities to these climatic refugia is of high potential to not only maintain unique elements of biodiversity, but protect safe havens where species can survive under changing environmental conditions. While most inferences of biodiversity refugia require detailed information about past dispersal our molecular data for focal taxa, which limits their taxonomic and spatial extent (reviewed in Keppel et al., 2012), our results suggest that an understanding of the processes that define refugia (e.g. climate stability during the Quaternary) based on readily available palaeoclimatic and diversity data will allow to extend...
the identification and protection of refugia for biota under past and future climate change to the global scale.

5 | CONCLUSIONS

By predicting species richness and rarity based on their relationships with contemporary climate and with climatic changes since the LGM, we showed that the congruence in species richness and rarity patterns across taxa is mainly driven by similar responses to the contemporary climate, whereas the underlying signatures of Quaternary climatic changes are less similar. Nevertheless, these palaeoclimatic changes seem to have left a strong imprint on biodiversity. Thus, our results demonstrated that regions characterized by a high climate stability during the Quaternary harbour a disproportionately high diversity and we showed that these regions are rather poorly covered by established protected areas. We thereby exemplified the potential of models incorporating climate stability during the Quaternary for understanding biodiversity patterns and for identifying conservation areas of major importance for the survival of biodiversity based on readily available data. Identifying such biodiversity refugia might be particularly relevant for taxa and regions were large-scale priority setting is currently based on species richness and rarity alone, because of the strong inherent correlation of these commonly used diversity measures and their strong relationships with the contemporary climate that obscure the signature of historical factors underlying biodiversity patterns.

ACKNOWLEDGEMENTS

The authors thank Roman Fricke for fruitful discussions and Katherine M. Bannar-Martin for comments on an earlier version of the manuscript. Open access funding enabled and organized by Projekt DEAL.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13134.

DATA AVAILABILITY STATEMENT

The assemblage-level data that support the findings of this study are available from Dryad Digital repository at https://doi.org/10.5061/dryad.nk98s37r5. These data were derived from the following resources (available upon request): IUCN (2016), BirdLife International & NatureServe (2015), Clausnitzer et al. (2012).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Pinkert S, Zeuss D, Dijkstra K-DB, et al. Climate–diversity relationships underlying cross-taxon diversity of the African fauna and their implications for conservation. Divers Distrib. 2020;26:1330–1342. https://doi.org/10.1111/ddi.13134