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Protected areas and the conservation of African bat diversity

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ABSTRACT

Lack of knowledge on biodiversity hinders the inclusion of multiple diversity metrics in conservation programs, especially for tropical regions and neglected taxa. Here, using high resolution data (1 km^2), we evaluate the representativeness of the protected areas (PAs) for the conservation of African bats considering taxonomic (TD), phylogenetic (PD), and functional (FD) diversity (calculated using Hill numbers), range-size rarity richness (RAR; calculated using the species' distribution range). For each index, we identified the hotspots of diversity by fitting a generalized additive model with TD as explanatory variable. Areas with positive residuals and significant z-scores were defined as hotspots of diversity. Using Zonation, we measured the coverage provided by PAs and identified the top priority non-protected areas. Hotspots of PD are concentrated in the Sahel belt and in Congo, while the west coast and southern Africa are important for FD. RAR is strongly concentrated in Madagascar. The existing PAs cover 13% of the continent, and, on average, 17% of each diversity index, with 80% of the species being covered from 10% to 25%. Expanding the existing PAs to a 30% target could ensure the conservation of 77% of all diversity indices, with 59% of the species covered for more than 75% of their distribution range. While existing PAs do not offer a reasonable protection to the diversity of African bats, the new priority areas that we identified could be considered by future efforts to improve the conservation of an important component of biodiversity.

1. Introduction

Biodiversity plays a crucial role in supporting human well-being by providing fundamental goods and services such as food, clean water, climate mitigation, recreation, and many others (Díaz et al., 2018). However, human activities are leading to a decline in global biodiversity, with climate change that, acting in synergy with other threats, is accelerating the process of biodiversity loss (Johnson et al., 2017). Therefore, conserving biodiversity is clearly a priority if we want to avoid irreversible species loss and the related socio-economic consequences (Isbell et al., 2017; O'Connor et al., 2021).

Species richness (or taxonomic diversity, TD) has been widely used to develop large scale, spatially explicit conservation strategies (Myers et al., 2000; Jetz et al., 2004; Marshall et al., 2020), but there is now a general consensus on the need to focus our efforts on multiple facets of biodiversity (Pollock et al., 2017). Considering TD, and particularly the diversity of endemic and/or endangered species, we could account for the current diversity and rarity of species; considering also phylogenetic diversity (PD; Faith, 1992) and functional diversity (FD; Petchey and Gaston, 2002), we could consider both the evolutionary history and the ecosystems' functions and services provided by species and communities (Mazel et al., 2014; Zupan et al., 2014; Harvey et al., 2017).

A practical example of how PD can be used in conservation prioritization is the EDGE framework (Isaac et al., 2007) which is one of the first conservation program aiming at the protection of species' evolutionary distinctiveness (measured as PD) and it has been followed by several studies (e.g., Pollock et al., 2015; Rosauer et al., 2017; Pipins et al., 2024). Along the same line, a number of analyses included FD into some type of conservation planning by considering traits related to ecosystem functioning, and acknowledging the importance of considering more aspects of the tree of life besides the simple sum of species (Thuiller et al., 2015; Pollock et al., 2017; Pollock et al., 2020; Faith, 2021). In the last few years, the diversity of species interactions has been included in large scale conservation studies considering European terrestrial vertebrates (Ceron et al., 2023; Gaüzère et al., 2022; Gaüzère et al., 2023), although its inclusion is still hindered by the scarcity of available data (but see Maiorano et al., 2020).

However, if theoretically there is a general agreement on the

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importance of focusing on multiple facets of biodiversity, the knowledge of biodiversity that we have is still limited and often biased (Hortal et al., 2015). For many taxa and geographical regions, implementing conservation strategies based on multiple facets of biodiversity is not feasible at all, and this is true especially for the regions that host the highest biodiversity like tropical areas (e.g., the Congo basin in central Africa, the Amazon basin in South America, many rainforests in Southeast Asia; Titley et al., 2017; Culumber et al., 2019; García-Roselló et al., 2023). Many tropical areas are under-sampled compared to temperate regions despite being the areas with the highest levels of biodiversity (Oliver et al., 2021; Šmíd, 2022). Both geographic and socio-economic factors often result in lower inventory completeness (Meyer et al., 2015; Hughes et al., 2021; Cosentino and Maiorano, 2021) and implementing any coordinated and informed conservation program in areas which are poor, remote, and politically unstable is hard even considering TD only, leaving aside all other different aspects of biodiversity (Pollock et al., 2020). Taxonomically, these regions host an incredible biodiversity of invertebrates and small vertebrates; these represent by far the bulk of all living beings (Rocha-Ortega et al., 2021; Šmíd, 2022) but are only marginally known, especially when compared to larger vertebrates and vascular plants which are over-represented in the literature. This bias is driven by intrinsic features of the organisms (e.g., species rarity and/or detectability), by taxonomic research, that invests more effort in threatened species, and by societal preferences, with citizen-science programs that may have amplified this bias towards charismatic taxa (Troudet et al., 2017; Di Marco et al., 2017).

The African continent, except for South Africa, is basically unknown even compared to other tropical areas (e.g., South America and Asia; Catullo et al., 2008; Llorente-Culebras et al., 2023). Most studies on biodiversity and conservation considering Africa are focused on a few countries (e.g., Uganda, Tanzania, and South Africa; Llorente-Culebras et al., 2023) resulting in a lack of knowledge when looking at the continental scale. Taxonomically, even for well-known groups of vertebrates such as birds and mammals, conservation efforts are strongly biased towards charismatic species (e.g., large mammals) while other taxa (e.g., small mammals) are almost always overlooked (Albert et al., 2018; Tam et al., 2022).

Focusing on mammals in Africa, bats (Chiroptera) are vastly understudied compared to other taxa (Martínez-Fonseca et al., 2024), although the African continent harbors almost 20% of all bat species (Burgin et al., 2018; Monadjem et al., 2024). With 320 species, 60 genera, and 13 families (Wilson and Mittermeier, 2019), African bats occupy a huge variety of ecological niches (Cosentino et al., 2023a), ranging from insectivores (almost 87% of the species) to frugivores and nectarivores (almost 13% of the species), with species being able to prey on other vertebrates (bats included; e.g., *Nycteris grandis*). African bats provide valuable ecosystem services, going from pest control to pollination and seed dispersal (Kunz et al., 2011; Boyles et al., 2011), but they also carry a higher proportion of zoonotic viruses compared to other mammals (Luis et al., 2013; Olival et al., 2017), making their monitoring particularly important for zoonotic disease risk mitigation (Markotter et al., 2020; Koch et al., 2020).

Despite the important value of bats for both biodiversity and human well-being, bats are threatened by habitat loss and fragmentation, human disturbance and global warming, and many larger species are actively hunted for the bushmeat trade (Mickleburgh et al., 2009; Frick et al., 2019). Of roughly 300 species occurring in Africa, 27% are ‘Data Deficient’ or ‘Not Evaluated’ in the IUCN Red List of threatened species (Wilson and Mittermeier, 2019), and the lack of knowledge on the ecology and distribution of this group of mammals strongly hinder any conservation program.

In the last decade, few studies have investigated the patterns of species richness for African bats, often considering a local to regional scale or, at most, focusing on sub-Saharan Africa only (Schoeman et al., 2013; Tanshi et al., 2022; Monadjem et al., 2023). The hotspots of species diversity for African bats are all bounded between 10° north and 10° south (e.g., Herkt et al., 2016), with the richest areas corresponding to central African forests, savannas, and highlands (e.g., mount Cameroon, the Bamenda highlands, the eastern Arch Highlands, and the Ethiopian highlands). However, the few papers available in the current literature only focus on one single aspect of diversity, considering only TD (Herkt et al., 2016; Schoeman and Monadjem, 2018), or PD (Pio et al., 2014), or FD (Monadjem et al., 2018). Particularly limited is our knowledge on the degree of protection for African bats (Cooper-Bohannon et al., 2016; Smith et al., 2016). While we know the coverage offered to single species by protected areas in south-Saharan Africa (Montauban et al., 2025), we know nothing in terms of protected areas and functional and/or evolutionary diversity, and we do not have a complete picture of the continent for bat conservation. In fact, at the continental scale, no study has implemented a gap analysis considering the multifaceted diversity of African bats, and the scattered existing protected areas may not be sufficient for their protection, especially considering their dispersal abilities and long-range migratory movements (Popa-Lisseanu and Voigt, 2009). This underlines the urgency of studying this taxon in a continent undergoing fast and strong changes in land-use and with a human population growth that is among the fastest globally (Ezeh et al., 2020).

In this context, we aim to evaluate the representativeness of the current network of protected areas (PAs) for the conservation of African bats considering different facets of their diversity. For this purpose, we (i) identify hotspots of multifaceted diversity of African bats including taxonomy, rarity, phylogeny and ecological functionality; (ii) measure the coverage provided to these hotspots by the existing PAs; (iii) identify priority areas to close the gaps for the conservation of African bats. Focusing on the hotspots of multifaceted diversity, we expect to provide new areas of conservation importance for African bats never reported by different approaches (e.g., single-species prioritization analysis), highlighting the importance of focusing our conservation efforts on areas embedding assemblages with unique functionality and evolutionary history.

2. Methods

2.1. Study area, species list, and protected areas network

Our study area covers the entire African continent including Sinai, Madagascar, and all the other off-shore islands (Canaries, Cape Verde, Comoro, Seychelles, Reunion, Mauritius, and the Gulf of Guinea islands; Fig. S1 in Supplementary Material). Following the taxonomy in Wilson and Mittermeier (2019) and the data in Cosentino et al. (2023a), we overlapped the distribution range of all African bats with our study area and limited our analyses to 238 species endemic or sub-endemic (species with ≥95% of their distributions in our study area; distribution ranges obtained from Marsh et al., 2022). In this way, we excluded from the analyses species which occur in Africa but have a Palearctic (e.g., *Hypsugo savii*) or Indomalayan (e.g., *Taphozous* spp.) distribution, species which would have inflated the level of diversity along the boundaries of our study area and which cannot be conserved in African protected areas alone.

We obtained data on African PAs from the World Database on Protected Area (WDPA, www.protectedplanet.net) considering all PAs with management categories specifically aimed at the support and conservation of biodiversity. We included both polygon and point data to consider as many PAs as possible. From the original database, we excluded all “proposed”, “adopted”, and “not reported” PAs, as well as other effective area-based conservation measures (OECM), marine PAs, and areas with “not applicable” management category. For point data, we created a circular buffer with an area corresponding to the reported area in the WDPA.

2.2. *Phylogenetic, functional, and distribution data*

Following the methods in Cosentino et al. (2023a), we obtained from Upham et al. (2019) 100 phylogenetic node-based trees together with source trees estimated from either DNA or morphology ('complete trees') to include as many species as possible in the analysis. All cases of taxonomic inconsistencies and/or synonymy between our list of species and Upham et al. (2019) are described in Cosentino et al. (2023a; Table S9 in the Supplementary Information). We selected from the AfroBaT dataset (Cosentino et al., 2023a) a set of traits covering morphology, reproduction, life-history, and trophic ecology. We assumed that these categories represent informative niche dimensions linked to ecosystem functions (Violle et al., 2007; Patterson et al., 2003; Table S2). The AfroBaT dataset includes both imputed data and data truly available in the literature. We recognize that the inclusion of imputed data may introduce uncertainties in our results. However, Cosentino et al. (2023a) used a carefully planned imputation procedure to decrease the level of uncertainty in their results. Furthermore, considering the final set of traits that we selected for the calculation of FD, almost half of the species (44.5%) had true (not imputed) trait data, clearly supporting the reliability of our conclusions. For each trait category, we performed a principal component analysis (*FactoMineR* R package; R 4.1.2) and selected from the original dataset the minimum number of representative traits covering most of the variance in the data (at least 70% of the variance; Fig. S3). From these, we summarized variables representing the same functional trait (see Table S2 for details) considering the biological and ecological characteristics of the taxon. Considering all traits for all categories, we further excluded those with a Pearson correlation $\geq |0.7|$ (Dormann et al., 2013), obtaining a final set of 10 functional traits (forearm length, total gestation length, lactation length, reproductive delay, migratory, colony size, activity pattern, roost type, trophic guild, and number of diet items; Table S2).

We obtained a species distribution model for each species from Cosentino et al. (2023a). In particular, for 146 species we obtained a continuous species distribution model (SDM); all modelling details are available in Cosentino et al., 2023b. We converted these SDMs into a binary prediction using a species-specific threshold maximizing the true skill statistics (TSS; Liu et al., 2016). For 92 species with a narrow distribution, we obtained from the same source a bioclimatic envelope model (Cosentino et al., 2023a), and we classified as 'presence' all pixels with a probability of presence >0. We focused our spatial analyses on models (either SDMs or climate envelopes) to minimize the effect of the important gaps existing in the data. Furthermore, models minimize the spatial gaps obviously present in expert-based range maps, while improving the spatial resolution for conservation planning studies and filling in poorly known or non-surveyed areas (Prieto-Torres et al., 2018), which are the rule in Africa.

2.3. *Diversity indices analysis*

To compute TD, PD, and FD, we followed the framework based on Hill numbers proposed by Chao et al. (2014a). This framework integrates species richness and, if available, species abundance in the calculation of diversity indexes while accounting for sampling bias and variance in the distribution of species abundance. In fact, the observed species richness is usually underestimated due to the presence of rare species and to the high sensitivity of any measurement of species richness to the area being surveyed. Moreover, species richness does not consider the relative abundance of each species, ignoring differences among rare and common species within the assemblages (see Chao et al., 2014b). These issues are very important in bats, which form colonies with seasonal variations in their abundance due to migratory behaviors (especially common in frugivore bats) and to the dynamics of nursery colonies (during the weaning period) and hibernating colonies (during the winter period; Kunz et al., 2003). In this context, obtaining a reliable sample of the species' abundance is highly problematic, and the Hill numbers framework (Hill, 1973; Jost, 2007) allows to tackle or, at least, minimize these problems. Considering the taxonomic diversity, Hill numbers for sample-based incidence data measure the effective number of taxonomic entities (species) in the assemblage. This approach has been extended to include both the species evolutionary history (Chao et al., 2010) and species functional distances (Chiu and Chao, 2014).

We computed all diversity indices in each 1×1 km cell considering a species as present or absent (see distribution data above). TD is calculated as the number of species within each cell, PD is the sum of the branch lengths (average across 100 trees) of the phylogenetic tree connecting all species present in each cell (Faith, 1992), FD is the sum of functional pairwise Gower distances between all species in each cell (Pavoine et al., 2009).

We also computed an index of diversity based on the range-size rarity (RAR) for each pixel; in particular, we weighted the distribution of each species by their global geographic ranges (Marsh et al., 2022), by assigning to each pixel classified as presence for a species the inverse range size. We rescaled all diversity indices from 0 to 100 by dividing by the maximum value of the index and then multiplying by 100.

Considering that PD, FD, and RAR are intrinsically linked to TD (Davies and Buckley, 2012), we fitted a generalized additive model (GAM) using each index as response and TD as explanatory variable. TD was included in the model as both a linear and a quadratic term and, to account for spatial autocorrelation, we also included geographic coordinates as a smooth factor (Wood, 2006). Then, we calculated the z-scores of the residuals to identify the areas with values of PD, FD, and RAR higher than expected given TD. All areas with positive z-scores were classified as hotspots of diversity for PD, FD, and RAR.

2.4. *Gap analysis of multifaceted diversity*

To evaluate the representativeness of the current PAs for the conservation of African bats, we performed a two-steps analysis using Zonation (v5; Moilanen et al., 2022): first we measured the coverage provided by the existing PAs to the diversity of African bats, and then we identified the areas outside the current PAs network that should have the highest priority for the conservation of African bats (Mikkonen and Moilanen, 2013). We included in the analyses the four diversity indexes (TD, FD, PD, and RAR) described above. To explicitly account for the conservation status of each species in the prioritization analysis, we weighted the TD layer by using a species-specific weight calculated from the IUCN Red List categories, using for each species the following multipliers: 1 = Least Concern (LC); 2 = Near Threatened (NT); 3 = Vulnerable (DD), Data Deficient (DD), and Not Evaluated (NE); 4 = Endangered (EN); 5 = Critically Endangered (CR). To identify the priorities for the expansion of the existing PAs, we computed a complementarity-based ranking of conservation priority based on the four diversity indexes by progressively discarding locations with lower biodiversity values until the entire study area has been assessed (Lehtomäki and Moilanen, 2013). We performed all analyses using the core-area zonation (CAZ2) marginal loss algorithm (Moilanen et al., 2005), which focuses on the areas with the highest conservation value. To check for the robustness of our results to the choice of the algorithm, we also performed the same analyses considering the additive-benefit function (ABF) algorithm (Moilanen et al., 2005) which focuses more on species richness.

Zonation produces two main outputs: performance curves, which quantify how much of the features' distributions are covered at different priority levels, and priority rank maps, in which each pixel is ranked from highest to lowest priority (Moilanen et al., 2022). We ran a first priority rank analysis, hereafter the 'unconstrained analysis', in which we considered the entire study area as included in the ranking. We also ran a second priority rank analysis, hereafter the 'hierarchical analysis', in which we constrained the ranking within the existing PAs, therefore forcing the top priorities into existing PAs irrespective of their biodiversity values while implementing the usual ranking procedure for the rest of the study area. From the unconstrained analysis we obtained the desirable network of areas that should be protected in Africa to conserve all facets of diversity of bats, assuming that the existing PAs do not represent a constraint and that the national boundaries and the lack of international cooperation do not impede a coordinated conservation planning. From the hierarchical analysis we obtained the top priority non-protected areas that should be added to the current PAs to fully protect bat diversity in Africa (Lehtomäki et al., 2019). For both analyses we set our conservation target to 30%, aligning our analyses with the conservation goals defined by the Global Biodiversity Framework (Woodley et al., 2019). Furthermore, we evaluated the coverage provided to the single species by both the current PAs network and by the current PAs plus the top priority expansion areas.

3. Results

Both linear and quadratic regression showed that RAR, PD, and FD were positively related to TD (RAR: $R^2 = 0.5$, $p < 0.0001$; PD: $R^2 = 0.9$, $p < 0.0001$; FD: $R^2 = 0.9$, $p < 0.0001$; Table S4; see Table S5 for results of quadratic model).

The Congo basin, including the west coast (from Ivory Coast to Cameroon), the Ethiopian plateau, and the Rift Valley were important for all diversity indices (Fig. S6). However, the hotspots of RAR included also areas in Gabon, Tanzania, and particularly in Madagascar (Fig. 1A), areas that are not considered by any other diversity measure. The hotspots of PD and FD gave an almost opposite spatial pattern (Fig. 1B and C). PD had its hotspots in the Mediterranean, in the Sahel belt (from Senegal up to Eritrea), and in Congo, all areas where FD was lower than expected. FD had its hotspots in the west coast (from Ivory Coast to Cameroon), in Uganda, Ethiopia, Tanzania, and in southern Africa (Botswana, Namibia, South Africa).

The results obtained with the CAZ2 and ABF algorithms overlapped very closely; we here refer to the results obtained with the CAZ2 algorithm; those obtained with the ABF algorithm are presented in Supplementary Material (Figs. S9, S10, S11, S12). The PAs included in our database represent the 13% of the continent, covering on average 17% for all diversity indices (Fig. 2A). Ideally, with the same level of coverage (13%), it would be possible to cover up to 56% on average of the diversity indices (Fig. 2B), clearly showing how limited and inefficient the current system of PAs is. Setting a 30% target, it would be possible to cover up to 84% of the high rank conservation areas (Fig. 2B) in the unconstrained analysis, while the average coverage would decrease to 77% in the hierarchical analysis (Fig. 2A).

The areas that should be considered to expand the current PAs system are distributed mostly in equatorial Africa and along the south-eastern valleys (Fig. 3). A few small areas are also present in the Mediterranean, but it's important to note that basically the entire Ethiopian plateau and almost all Madagascar should be protected if we want to achieve a 30% conservation target. In particular, the top 10% priority expansion areas are concentrated along the central plateau in Madagascar and the Ethiopian plateau in continental Africa. Particularly important are all the Rift Valley and the west coast (Somalia, Kenia, and Tanzania). The ideal distribution of protected areas without any spatial and/or political constraint and with a 30% conservation target is available in Fig. S7.

Most of the species (80%; $n = 190$) have between 10% and 25% of their ranges protected by the current PAs network (Fig. 4). Only a few species (5%; $n = 12$) reach a coverage between 25% and 50%, while just one species goes over 50% of its range covered by PAs. If we add the priority expansion areas to the current PAs, 31% of the species ($n = 74$) would have more than 50% of their distribution range covered, and 59% of the species ($n = 141$) would reach a coverage exceeding the 75% of their distribution. If we consider the results of the unconstrained analysis (Fig. S8) more than 73% of the species ($n = 175$) would be covered for more than 75% of their distribution.

4. Discussion

Despite the efforts to consider multiple aspects of biodiversity in conservation planning, the current state of biodiversity knowledge represents a huge practical constraint, especially for regions poor, remote, and politically unstable (e.g., Africa) and for taxa (e.g., bats) that are less appealing to the general public and more difficult to study for their intrinsic characteristics (e.g., detectability) (Martínez-Fonseca et al., 2024; Frick et al., 2019). In the last few years, several studies investigated the multiple facets of bats' diversity focusing mainly on neotropical (e.g., Carvalho et al., 2021; López-Baucells et al., 2022) or paleotropical bats (e.g., Tanshi et al., 2022), with African bats almost

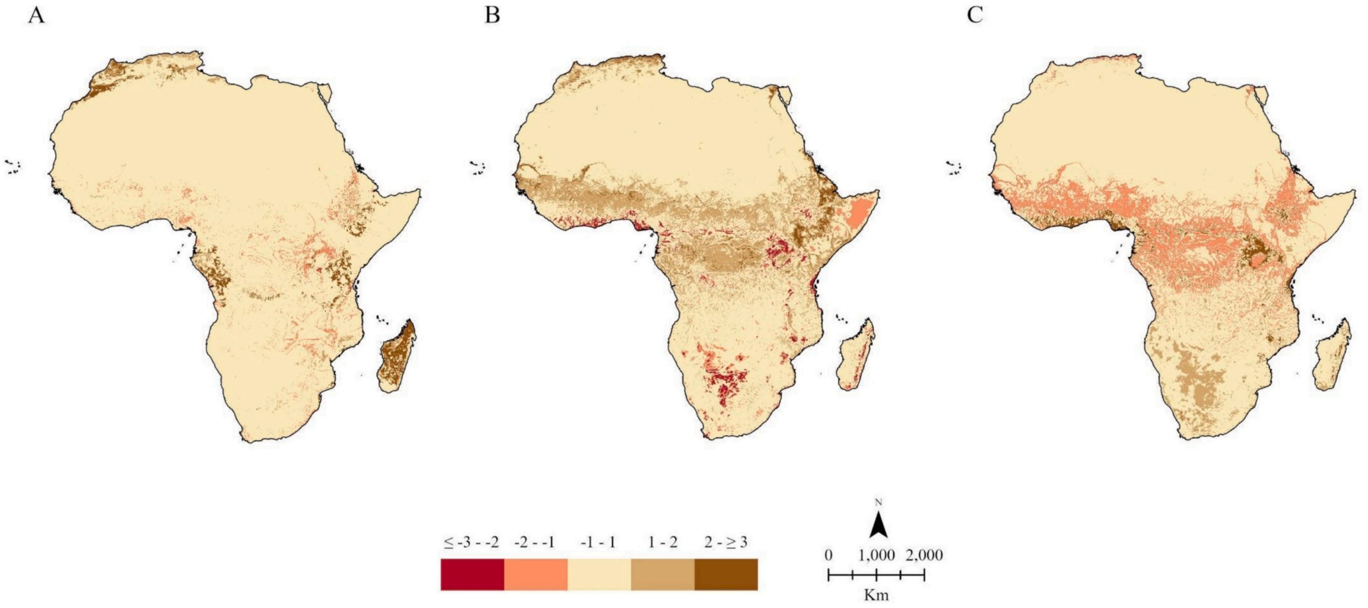

Fig. 1. Hotspots of RAR (A), PD (B), and FD (C). Shades of brown (positive values) depict the areas where the index has values higher than expected given TD, while shades of red (negative values) represent areas with values lower than expected given TD. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

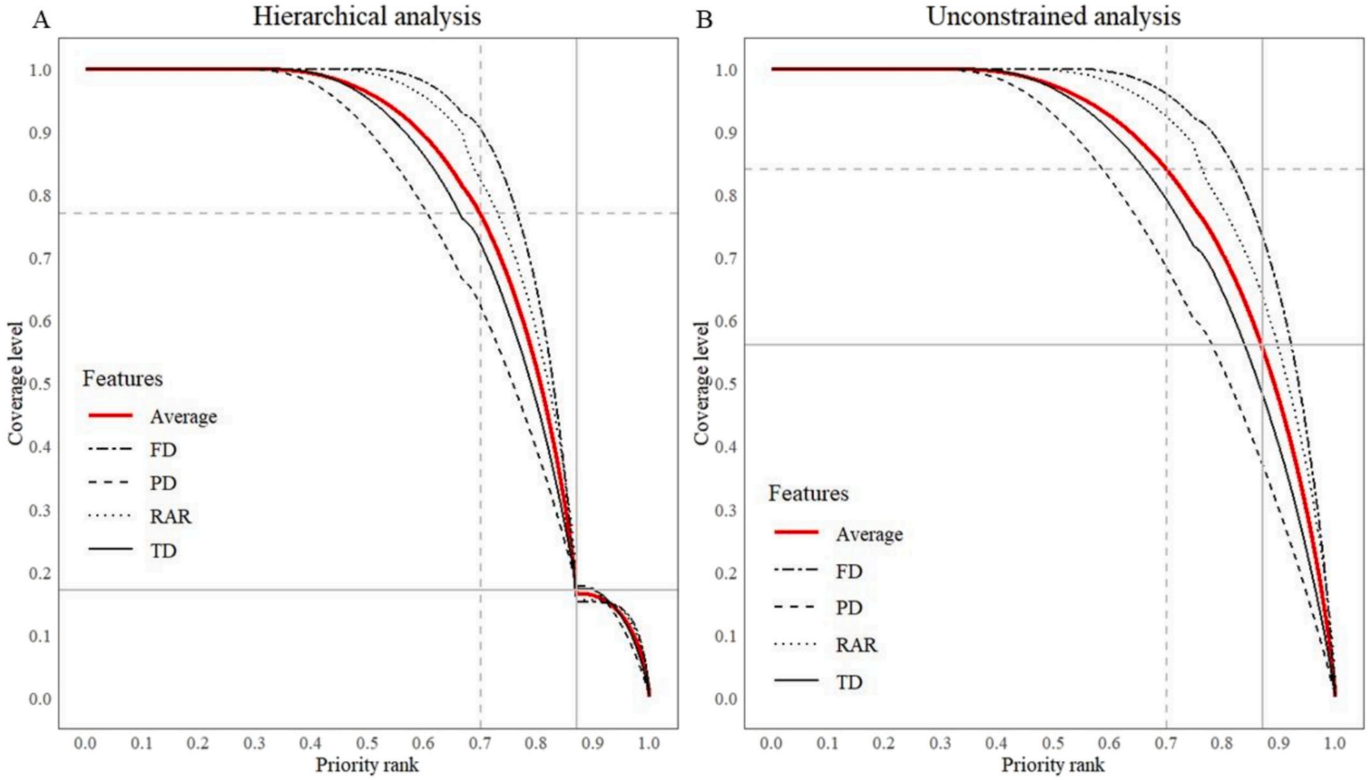

Fig. 2. Performance curves for the hierarchical (A) and unconstrained (B) analyses. The red line in each graph represents the average between all diversity features. In both panels, the solid lines identify the values corresponding to the 13% coverage offered by existing PAs while the dotted lines correspond to the 30% target. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

completely neglected. Smith et al. (2016) provided an interesting exception, focusing on current and future priority areas for the conservation of African bats; however, they focused only on taxonomic diversity with all problems related to that (Fletcher et al., 2025). Recently, Monadjem et al. (2023) investigated three aspects (taxonomic, functional, and phylogenetic) of beta diversity for Sub-Saharan bats but without any specific conservation aim. Finally, Montauban et al. (2025) performed a traditional, species-specific gap analysis, but again focusing only on Sub-Saharan bats.

To our knowledge, our study is the first to provide a gap analysis for the conservation of African bats considering their multifaceted diversity (TD, PD, FD, and RAR) at 1 km^2 resolution and considering the entire continent, from the Mediterranean coast up to southern Africa. Our findings clearly showed that the hotspots of diversity for African bats are poorly protected within the current PAs network, identifying also new priority areas not yet considered in the literature. Previous studies (e.g., Herkt et al., 2016; Smith et al., 2016; Monadjem et al., 2018) identify the Mediterranean and the equatorial Africa as important for endemisms and species richness. With our results, we have been able to highlight that the Mediterranean, the Congo basin, the Ethiopian mountains, and East African rift are hotspots for phylogenetic diversity and their conservation is fundamental to preserve the evolutionary history of the entire group. The west coast, large parts of Ethiopia, Uganda, and south Kenya are important as they host strictly endemic species (e.g., *Asellia patrizii*, *Rhinopoma macinnesi*, *Taphozous hamiltoni*), and the loss of these species in these areas would correspond to their global extinction. A similar consideration can be done for Madagascar. This island hosts unique centres of endemism, with 32 endemic species (Cardiff and Jenkins, 2016), and with an entire endemic family (Myzopodidae), making this island particularly important as a center for evolutionary and functional diversity (Antonelli et al., 2022; Ralimanana et al., 2022).

The lack of correspondence between the hotspots of PD and those of FD is particularly interesting and the ‘phylogenetic gambit’ hypothesis (Faith, 1992; Mazel et al., 2018) is basically not working for African bats. In fact, although in the literature PD has been considered as a good proxy for FD, our findings showed a spatial mismatch between these two facets of diversity, and the idea that the conservation of areas with high phylogenetic diversity would maximize the protection of ecosystem functioning (Cadotte et al., 2008; Mazel et al., 2017) does not hold for African bats. A number of different hypotheses are possible on why this is the case. The hotspots of FD in southern Africa (Botswana, Namibia, South Africa) may reflect areas with recent diversification along different ecological axes, bearing high levels of ecosystem functions but having very limited importance from a phylogenetic point of view. Interestingly, this area has never been reported as an area of high diversity for bats in previous studies which were based only on taxonomic or phylogenetic diversity (Schoeman et al., 2013; Herkt et al., 2016; Pio et al., 2014; Cooper-Bohannon et al., 2016). The Sahel belt (from Senegal up to Eritrea), the Mediterranean areas, the Nile delta, and central Africa offer a completely different view. They represent hotspots of PD that may reflect areas of ancient diversification where a unique evolutionary history may be conserved (Isaac et al., 2007; Davies and Buckley, 2011). Many of these areas are characterized by riverine habitats which are extremely important for bats in subtropical savanna and arid environments not only as a source of water but also for foraging and commuting (Herkt et al., 2016; Monadjem and Reside, 2008; Fahr and Kalko, 2011). The riparian vegetation offers both significant insect swarms and linear landscape elements where bats can move and migrate connecting populations of bats over hundreds of kilometers and facilitating the seasonal migrations undertaken by frugivorous bats (e.g., *Eidolon* spp., *Epomophorus*, *Myonycteris*). At the same time, these habitats offer apparently only limited options for different ecological niches, possibly because of their highly seasonal nature.

Given the limited funding available to expand or design new protected areas, especially in poor regions like the African continent,

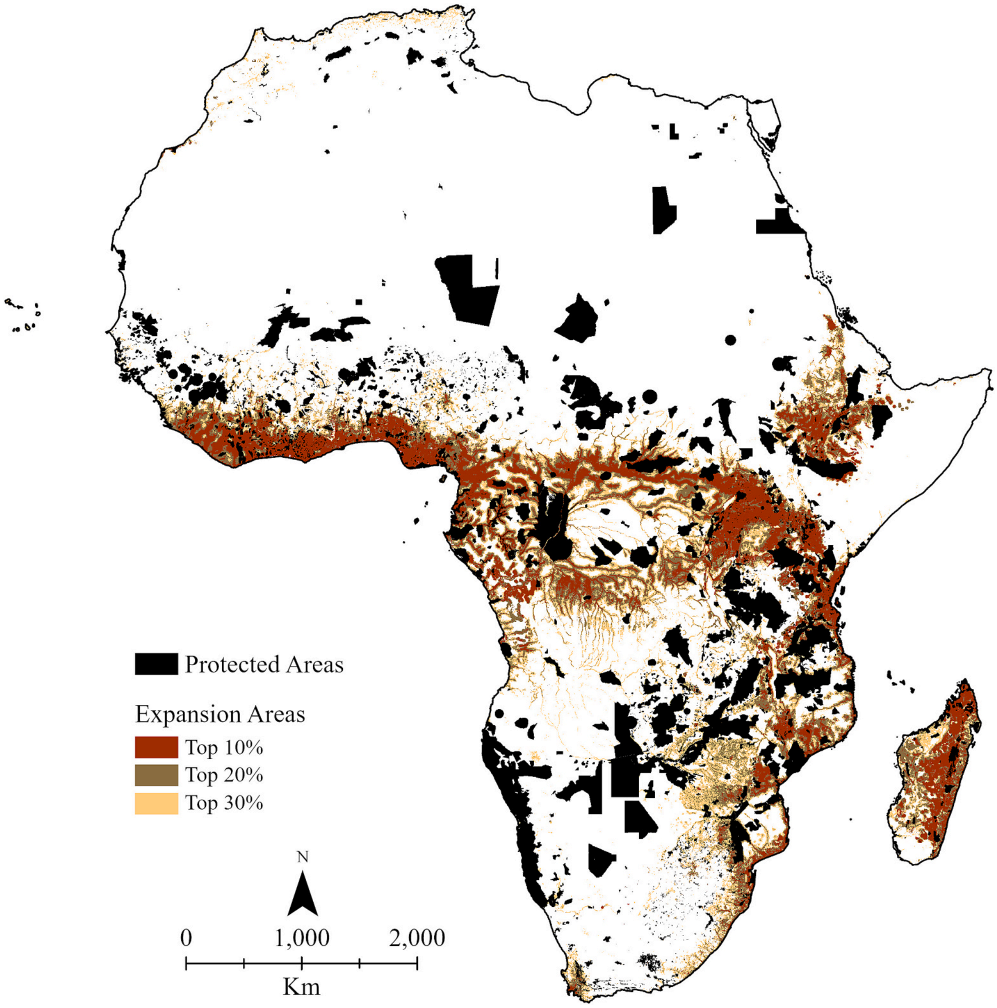

Fig. 3. Priority rank map for which the priority is constrained within the existing African PAs (hierarchical analysis). The dark brown color depicts the expansion areas with a priority rank greater or equal to 0.90 (the top 10% across the African continent), the light brown the expansion areas with a priority rank greater or equal to 0.80 (the top 20%), and the sand color the expansion areas with a priority rank greater or equal to 0.70 (the top 30%). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

considering multiple aspects of diversity allows the conservation of a given taxon to be optimized at the continental scale showing improvements for conservation planning also at the level of individual species. Most of the African PAs are defined along the old game reserves without specific conservation targets, with the only exception of the Cape Floristic Region of South Africa where more targeted conservation planning has been attempted (e.g., Pressey et al., 2003), but without considering bats. In fact, the hotspots of multifaceted diversity of African bats are poorly protected by the current PAs network, which covers on average only 17% of all diversity facets considered. In an ideal setting, assuming no political, geographical, and historical constraint, a much higher level of conservation would be possible, reaching an astonishing 56% of coverage for the diversity of African bats with only the 13% of territory being protected.

Our analyses clearly have a few drawbacks and a good space for improvement. First of all, in our list of species we have included only species that are endemic and/or subendemic of the African continent. In this way, we avoided inflating the level of richness along the boundaries of our study area, focusing strongly on the species that can be protected only in Africa. However, we recognize that we are losing part of the biodiversity of the region, with potentially important consequences for conservation. This choice could have an effect especially in a global change context, with species reshuffling their distribution even across continents (e.g., crossing the Mediterranean basin; Maiorano et al., 2013). Future analyses should carefully consider these aspects focusing more on the dynamics of biodiversity in time (e.g., Cancellario et al., 2022).

We did not consider in our prioritization any form of connectivity (either structural or functional). Although a spatially cohesive conservation network would often be desirable (Keeley et al., 2021), the level of knowledge on the spatial ecology of African bats is hugely limited, and any assumption on dispersal distances or space use would necessarily be based on a vastly incomplete knowledge, potentially biasing our results in unpredictable ways.

Furthermore, our findings do not include conservation recommendations at the level of single countries or provinces. Although an analysis considering the local scale is desirable to provide practical guidance for decision-makers, the current state of knowledge and the huge variability of the African continent in terms of environmental, social, economic, and political context hinder any effective and fair conservation planning at a continental scale and below. However, our findings may represent a starting point to shed light on new important conservation areas for African bats that could be considered in future works that include local social, political, and economic dynamics. In particular, we provided a map with different ranks of priority expansion areas that could help prioritize conservation interventions on the ground as a function of different resource availability or policy scenarios, allowing to focus on the most important priority areas when resources are scarce. Future

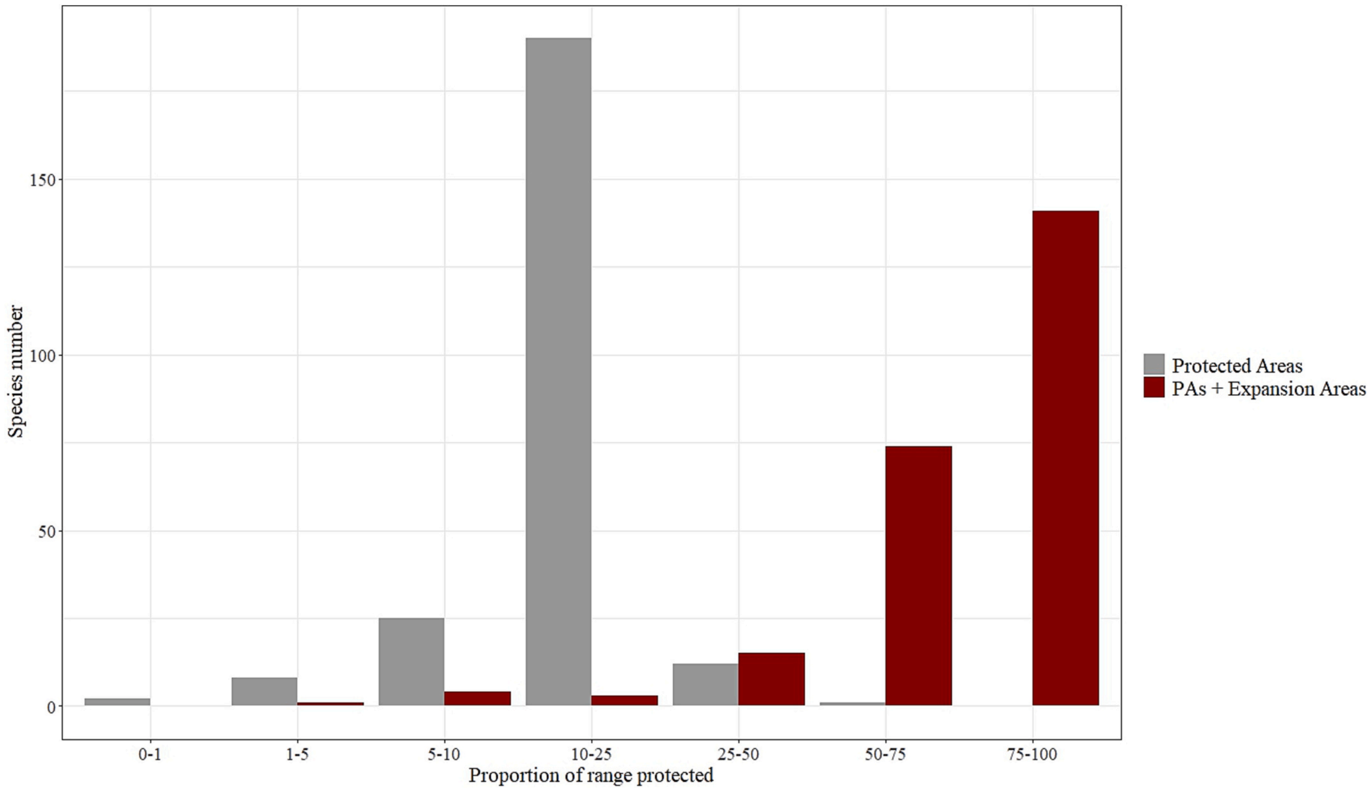

Fig. 4. Bar plot showing the number of species and the proportion of range protected by the current PAs network and by the PAs plus the expansion areas with a 30% conservation target.

analyses with fine scale data will better provide conservation directions directly to local managers and policy-makers to guide conservation actions at the regional level (e.g., Carvalho et al., 2025).

The priority rank map highlights how many key conservation areas are missing for African bats showing where the system of PAs should be enlarged. Currently, most of the areas along the equator belt (east coast, Uganda, Ethiopia, Tanzania), the Ethiopian plateau, and the Congo basin are not covered by protected areas which are located in areas at lower priority rank.

Many of these areas are extremely important also for other vertebrates as both conservation priorities and as research priorities (Nori et al., 2020), and a particular focus is certainly needed for Madagascar (which is important whatever aspect of biodiversity we consider; Antonelli et al., 2022) and the east African belt, particularly in Tanzania. The same is true for the equatorial belt which represents a must for the conservation of amphibians at global level (Bolochio et al., 2020), and a research priority for mammals, reptiles, and again amphibians (Nori et al., 2020). Moreover, despite the presence of PAs in these regions, several issues hinder their utility for biodiversity conservation. Unfavorable political conditions or human conflicts may lead to the lack of management of the PAs actually making them 'paper parks' leading to the extreme PADDD phenomenon ("Protected Area Downgrading, Downsizing and Degazettement") that is the decrease in the categorization, surface area and declassification of PAs (Mascia et al., 2014). Some designed PAs are managed for economic purposes such as hunting areas or classified forests for timber production. If on one hand, the extreme and uncontrolled poaching caused the almost total depletion of the animal populations especially in areas with dense forests ('empty forest syndrome'; Redford, 1992), on the other hand the statement 'if it pays, it stays' withstood for many years leading to benefits for the conservation of the hunted species. If the hunting was carried out in a sustainable manner, this could provide a certain degree of protection for the hunted species (UICN/PACO, 2009). However, the decrease in the number of animals due to the agro-pastoral encroachment led to the abandonment of the hunting areas becoming no longer profitable for hunting organizations (Chardonnet, 2019). Therefore, the progressive disappearance of big game hunting zones resulted actually in a decrease of protection for the hunted species. The trade-off of protecting a species with poaching is one of the 'elephant in the room' in conservation decisions in these hard geographical and political contexts (Macdonald and Willis, 2013).

Many of these trade-offs are linked to old management planning that does not fit anymore with the current pressures (Jones et al., 2018). Demographic growth inevitably led to direct and indirect consequences with the increasing human encroachment, bushmeat consumption, pollution of natural habitats, and so on. Even the buffer zone around PAs where hunting, deforestation, farming, and other similar activities were denied, has actually now disappeared. Furthermore, climate and land use changes with progressive desertification are just accelerating the deterioration of protected areas (Li et al., 2024). Africa today is already warmer than it was 100 years ago (Hulme et al., 2001), and it is going to experience important (and diverse) impacts from climate change. While Madagascar is projected to be (at least partially) a climate refugia, the equatorial belt is going to be heavily impacted, both in temperature and in precipitation. The importance of adaptation is widely recognized but many constraints are hindering the progress, particularly in low income settings (Adenle et al., 2017).

In this context, investing more efforts in monitoring the areas we identified is a key action to maximize the preservation of assemblages with a great evolutionary history and functionally different species. This is even more important considering the global change context we are facing, not only for the conservation of African bats but also for human health (Romanelli et al., 2015). Cave-dwelling (e.g., Hipposideridae) and frugivores (Pteropodidae) bats may be particularly threatened by the human population growth: the former for the increasing caves disturbance due to mining activities, guano harvesting, and tourism, and the latest for the escalation of conflicts with the fruit growers (Aziz et al., 2016; Frick et al., 2019). The projected rise in temperature on the African continent could lead to an increase in heatwaves and extreme climatic events that have already caused massive deaths in bat populations (Pruvot et al., 2019; McKechnie et al., 2021). On the other hand, climate change may lead to a habitat type shift with consequent changes in bat species richness which, combined with an increase in human population density, may increase the overlap between humans and wildlife with potential risk of spillover events (e.g., Beyer et al., 2021). Since over 70% of emerging infectious diseases (EIDs) originate from wildlife, the progressive reduction of available habitat for wildlife along with the human population growth could further increase this number (Carlson et al., 2022).

The new priority areas we identified highlight the need for better conservation of bat populations outside the already established African protected areas, promoting operational multidisciplinary conservation programs that include multiple facets of biodiversity in order to safeguard both wildlife and human health. However, the African continent represents a particularly difficult case study. Africa is the continent where our species have originated (Tattersall, 2009) and it is considered one of the last strongholds of biodiversity at the global level (25% of the global biodiversity hotspots as defined by Conservation International are completely or partially in Africa). Yet, its history, its political instability and fragmentation, and its uncertain and crowded future (Cilliers, 2021) clearly call for an international and coordinated conservation effort as the only resort we have to conserve its unique biodiversity.

CRediT authorship contribution statement

F. Cosentino: Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **L. Maiorano:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors have nothing to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111787.

Data availability

All data used for the analyses are already available online.

References

Adenle, A.A., Ford, J.D., Morton, J., Twomlow, S., Alverson, K., Cattaneo, A., Cervigni, R., Kurukulasuriya, P., Huq, S., Helfgott, A., Ebinger, J.O., 2017. Managing climate change risk in Adrica-A global perspective. Ecol. Econ. 141, 190–201.

Albert, C., Luque, G.M., Courchamp, F., 2018. The twenty most charismatic species. PloS One 13 (7), e0199149.

Antonelli, A., Smith, R.J., Perrigo, A.L., Crottini, A., Hackel, J., Testo, W., Farooq, H., Torres Jiménez, M.F., Andela, N., Andermann, T., Andriamanohera, A.M., Andriambololonera, S., Bachman, S.P., Bacon, C.D., Baker, W.J., Belluardo, F., Birkinshaw, C., Borrell, J.S., Cable, S., Canales, N.A., Carrillo, J.D., Clegg, R., Clubbe, C., Cooke, R.S.C., Damasco, G., Dhanda, S., Edler, D., Faurby, S., de Lima Ferreira, P., Fisher, B.L., Forest, F., Gardiner, L.M., Goodman, S.M., Grace, C.M., Guedes, T.B., Henniges, M.C., Hill, R., Lehmann, C.E.R., Lowry II, P.P., Marline, L., Matos-Maraví, P., Moat, J., Neves, B., Nogueira, M.G.C., Onstein, R.E., Papadopulos, A.S.T., Perez-Escobar, O.A., Phelps, L.N., Phillipson, P.B., Pironon, S., Przelomska, N.A.S., Rabarimanarivo, M., Rabehevitra, D., Raharimampionona, J., Rajaonah, M.T., Rajaonary, F., Rajaovelona, L.R., Rakotoarinivo, M., Rakotoarisoa, A.A., Rakotoarisoa, S.E., Rakotomalala, H.N., Rakotonasolo, F., Ralaiveloarisoa, B.A., Ramirez-Herranz, M., Randriamamonjy, J.E.N., Randriamboavonjy, T., Randrianasolo, A.V., Rasolohery, A., Ratsifandrihamanana, A.N., Ravololomanana, N., Razafiniary, V., Razanajatovo, H., Razanatsoa, E., Rivers, M., Sayol, F., Silvestro, D., Vorontsova, M.S., Walker, J., Walker, B.E., Wilkin, P., Williams, J., Ziegler, T., Zizka, A., Ralimanana, H., 2022. Madagascars extraordinary biodiversity: evolution, distribution, and use. Science 378 (6623), eabf0869.

Aziz, S.A., Olival, K.J., Bumrungsri, S., Richards, G.C., Racey, P.A., 2016. The conflict between pteropodid bats and fruit growers: species, legislation and mitigation. In: Bats in the Anthropocene: Conservation of Bats in a Changing World, pp. 377–426.

Beyer, R.M., Manica, A., Mora, C., 2021. Shifts in global bat diversity suggest a possible role of climate change in the emergence of SARS-CoV-1 and SARS-CoV-2. Sci. Total Environ. 767, 145413.

Bolochio, B.E., Lescano, J.N., Cordier, J.M., Loyola, R., Nori, J., 2020. A functional perspective for global amphibian conservation. Biol. Conserv. 245, 108572.

Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2011. Economic importance of bats in agriculture. Science 332 (6025), 41–42.

Burgin, C.J., Colella, J.P., Kahn, P.L., Upham, N.S., 2018. How many species of mammals are there? J. Mammal. 99 (1), 1–14.

Cadotte, M.W., Cardinale, B.J., Oakley, T.H., 2008. Evolutionary history and the effect of biodiversity on plant productivity. Proc. Natl. Acad. Sci. 105 (44), 17012–17017.

Cancellario, T., Miranda, R., Baquero, E., Fontaneto, D., Martínez, A., Mammola, S., 2022. Climate change will redefine taxonomic, functional, and phylogenetic diversity of Odonata in space and time. npj Biodiversity 1 (1), 1.

Cardiff, S.G., Jenkins, R.K., 2016. The bats of Madagascar: a conservation challenge. Lessons Conserv. 6, 80–108.

Carlson, C.J., Albery, G.F., Merow, C., Trisos, C.H., Zipfel, C.M., Eskew, E.A., Olival, K.J., Ross, N., Bansal, S., 2022. Climate change increases cross-species viral transmission risk. Nature 607 (7919), 555–562.

Carvalho, W.D., Lourenço, E.C., Costa, L.M., Bergallo, H.G., Esbérard, C.E.L., 2021. Patterns and drivers determining phyllostomid bat diversity in land-bridge islands off the south-east coast of Brazil. Biol. J. Linn. Soc. 134 (3), 604–619.

Carvalho, W.D., Guerrero, J.C., Bernard, E., Esbérard, C.E.L., Ditchfield, A.D., Gregorin, R., Laurindo, R.S., Mancini, M.C.S., Martins, M.A., Nobre, P.H., Srbek-Araujo, A.C., Vela-Ulian, C.M., Xavier, B.S., Romero, D., 2025. Bat distribution and habitat protection degree along an elevational gradient in the brazilian Atlantic forest. J. Biogeogr. 52 (10), e70023.

Catullo, G., Masi, M., Falcucci, A., Maiorano, L., Rondinini, C., Boitani, L., 2008. A gap analysis of Southeast Asian mammals based on habitat suitability models. Biol. Conserv. 141 (11), 2730–2744.

Ceron, K., Sales, L.P., Santana, D.J., Pires, M.M., 2023. Decoupled responses of biodiversity facets driven from anuran vulnerability to climate and land-use changes. Ecol. Lett. 26 (6), 869–882.

Chao, A., Chiu, C.H., Jost, L., 2010. Phylogenetic diversity measures based on Hill numbers. Philos. Trans. R. Soc. B: Biol. Sci. 365 (1558), 3599–3609.

Chao, A., Chiu, C.H., Jost, L., 2014a. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annu. Rev. Ecol. Evol. Syst. 45, 297–324.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014b. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological monographs 84 (1), 45–67.

Chardonnet, B., 2019. Reconfiguring the protected areas in Africa. Int. Union Conserv. Nat. Nat. Resour. 43 pages.

Chiu, C.H., Chao, A., 2014. Distance-based functional diversity measures and their decomposition: a framework based on Hill numbers. PloS One 9 (7), e100014.

Cilliers, J., 2021. The Future of Africa: Challenges and Opportunities. Springer Nature, p. 421.

Cooper-Bohannon, R., Rebelo, H., Jones, G., Cotterill, F., Monadiem, A., Schoeman, M.C., Taylor, P., Park, K., 2016. Predicting bat distributions and diversity hotspots in southern africa. Hystrix, Ital. J. Mammal. 27 (1).

Cosentino, F., Maiorano, L., 2021. Is geographic sampling bias representative of environmental space? Eco. Inform. 64, 101369.

Cosentino, F., Castiello, G., Maiorano, L., 2023a. A dataset on African bats' functional traits. Sci. Data 10 (1), 623.

Cosentino, F., Seamark, E.C.J., Van Cakenberghe, V., Maiorano, L., 2023b. Not only climate: the importance of biotic interactions in shaping species distributions at macro scales. Ecol. Evol. 13, e9855.

Culumber, Z.W., Anaya-Rojas, J.M., Booker, W.W., Hooks, A.P., Lange, E.C., Pluer, B., Ramírez-Bullón, N., Travis, J., 2019. Widespread biases in ecological and evolutionary studies. BioScience 69 (8), 631–640.

Davies, T.J., Buckley, L.B., 2011. Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. Philos. Trans. R. Soc. B Biol. Sci. 366 (1576), 2414–2425.

Davies, T.J., Buckley, L.B., 2012. Exploring the phylogenetic history of mammal species richness. Glob. Ecol. Biogeogr. 21 (11), 1096–1105.

Di Marco, M., Chapman, S., Althor, G., Kearney, S., Besancon, C., Butt, N., Maina, J.M., Possingham, H.P., von Bieberstein, K.R., Venter, O., Watson, J.E.M., 2017. Changing trends and persisting biases in three decades of conservation science. Global Ecol. Conserv. 10, 32–42.

Dìaz, S., Pascual, U., Stenseke, M., Martìn-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., Van Oudenhoven, A.P.E., van der Plaat, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Burkareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S., Shirayama, Y., 2018. Assessing nature's contributions to people. Science 359 (6373), 270–272.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46.

Ezeh, A., Kissling, F., Singer, P., 2020. Why sub-Saharan Africa might exceed its projected population size by 2100. Lancet 396 (10258), 1131–1133.

Fahr, J., Kalko, E.K., 2011. Biome transitions as centres of diversity: habitat heterogeneity and diversity patterns of West African bat assemblages across spatial scales. Ecography 34 (2), 177–195.

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61 (1), 1–10.

Faith, D.P., 2021. Valuation and appreciation of biodiversity: The "maintenance of options" provided by the variety of life. Front. Ecol. Evol. 9, 635670.

Fletcher, R.J., Green, R.E., Bladon, E.K., Atkinson, P.W., Phalan, B.T., Williams, D., Visconti, P., Balmford, A., 2025. Beyond species richness for biological conservation. Conserv. Lett. 18 (4), e13124.

Frick, W.F., Kingston, T., Flanders, J., 2019. A review of the major threats and challenges to global bat conservation. Ann. N. Y. Acad. Sci. 1469 (1), 5–25.

García-Roselló, E., González-Dacosta, J., Lobo, J.M., 2023. The biased distribution of existing information on biodiversity hinders its use in conservation, and we need an integrative approach to act urgently. Biol. Conserv. 283, 110118.

Gaüzère, P., O'Connor, L., Botella, C., Poggiato, G., Münkemüller, T., Pollock, L.J., Brose, U., Maiorano, L., Harfoot, M., Thuiller, W., 2022. The diversity of biotic interactions complements functional and phylogenetic facets of biodiversity. Curr. Biol. 32 (9), 2093–2100.

Gaüzère, P., Botella, C., Poggiato, G., O'Connor, L., Di Marco, M., Dragonetti, C., Maiorano, L., Renaud, J., Thuiller, W., 2023. Dissimilarity of vertebrate trophic interactions reveals spatial uniqueness but functional redundancy across europe. Curr. Biol. 33 (23), 5263–5271.

Harvey, E., Gounand, I., Ward, C.L., Altermatt, F., 2017. Bridging ecology and conservation: from ecological networks to ecosystem function. J. Appl. Ecol. 54 (2), 371–379.

Herkt, K.M.B., Barnikel, G., Skidmore, A.K., Fahr, J., 2016. A high-resolution model of bat diversity and endemism for continental Africa. Ecol. Model. 320, 9–28.

Hill, M., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. Annu. Rev. Ecol. Evol. Syst. 46 (1), 523–549.

Hughes, A.C., Orr, M.C., Ma, K., Costello, M.J., Waller, J., Provoost, P., Yang, Q., Zhu, C., Qiao, H., 2021. Sampling biases shape our view of the natural world. Ecography 44 (9), 1259–1269.

Hulme, M., Doherty, R., Ngara, T., New, M., Lister, D., 2001. African climate change: 1900-2100. Climate Res. 17 (2), 145–168.

Isaac, N.J., Turvey, S.T., Collen, B., Waterman, C., Baillie, J.E., 2007. Mammals on the EDGE: conservation priorities based on threat and phylogeny. PloS One 2 (3), e296.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G.M., Wardle, D.A., O'Connor, M.I., Duffy, J.E., Turnbull, L.A., Thompson, P.L., Larigauderie, A., 2017. Linking the influence and dependence of people on biodiversity across scales. Nature 546 (7656), 65–72.

Jetz, W., Rahbek, C., Colwell, R.K., 2004. The coincidence of rarity and richness and the potential signature of history in centres of endemism. Ecol. Lett. 7 (12), 1180–1191.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356 (6335), 270–275.

Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., Watson, J.E., 2018. One-third of global protected land is under intense human pressure. Science 360 (6390), 788–791.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88 (10), 2427–2439.

Keeley, A.T., Beier, P., Jenness, J.S., 2021. Connectivity metrics for conservation planning and monitoring. Biol. Conserv. 255, 109008.

Koch, L.K., Cunze, S., Kochmann, J., Klimpel, S., 2020. Bats as putative Zaire ebolavirus reservoir hosts and their habitat suitability in Africa. Sci. Rep. 10 (1), 14268.

Kunz, T.H., Lumsden, L.F., Fenton, M.B., 2003. Ecology of cavity and foliage roosting bats. In: Bat Ecology, 1. University of Chicago Press, pp. 3–89.

Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. Ann. N. Y. Acad. Sci. 1223 (1), 1–38.

Lehtomäki, J., Moilanen, A., 2013. Methods and workflow for spatial conservation prioritization using Zonation. Environ. Model. Software 47, 128–137.

Lehtomäki, J., Kusumoto, B., Shiono, T., Tanaka, T., Kubota, Y., Moilanen, A., 2019. Spatial conservation prioritization for the East Asian islands: a balanced representation of multitaxon biogeography in a protected area network. Divers. Distrib. 25 (3), 414–429.

Li, G., Fang, C., Watson, J.E., Sun, S., Qi, W., Wang, Z., Liu, J., 2024. Mixed effectiveness of global protected areas in resisting habitat loss. Nat. Commun. 15 (1), 8389.

Liu, C., Newell, G., White, M., 2016. On the selection of thresholds for predicting species occurrence with presence-only data. Ecol. Evol. 6 (1), 337–348.

Llorente-Culebras, S., Ladle, R.J., Santos, A.M., 2023. Publication trends in global biodiversity research on protected areas. Biol. Conserv. 281, 109988.

López-Baucells, A., Rowley, S., Rocha, R., Bobrowiec, P.E., Palmeirim, J.M., Farneda, F. Z., Meyer, C.F., 2022. Interplay between local and landscape-scale effects on the taxonomic, functional and phylogenetic diversity of aerial insectivorous neotropical bats. Landsc. Ecol. 37 (11), 2861–2875.

Luis, A.D., Hayman, D.T.S., O'Shea, T.J., Cryan, P.M., Gilbert, A.T., Pulliam, J.R.C., Mills, J.N., Timonin, M.E., Willis, C.K.R., Cunningham, A.A., Fooks, A.R., Rupprecht, C.E., Wood, J.L.N., Webb, C.T., 2013. A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? Proc. R. Soc. B Biol. Sci. 280 (1756), 20122753.

Macdonald, D.W., Willis, K.J., 2013. Elephants in the room: tough choices for a maturing discipline. In: Key topics in Conservation Biology, 2, pp. 467–494.

Maiorano, L., Amori, G., Capula, M., Falcucci, A., Masi, M., Montemaggiori, A., Pottier, J., Psomas, A., Rondinini, C., Russo, D., Zimmermann, N.E., Boitani, L., Guisan, A., 2013. Threats from climate change to terrestrial vertebrate hotspots in europe. PLoS One 8 (9), e74989.

Maiorano, L., Montemaggiori, A., Ficetola, G.F., O'connor, L., Thuiller, W., 2020. TETRA-EU 1.0: a species-level trophic metaweb of European tetrapods. Glob. Ecol. Biogeogr. 29 (9), 1452–1457.

Markotter, W., Coertse, J., De Vries, L., Geldenhuys, M., Mortlock, M., 2020. Bat-borne viruses in Africa: a critical review. J. Zool. 311 (2), 77–98.

Marsh, C.J., Sica, Y.V., Burgin, C.J., Dorman, W.A., Anderson, R.C., del Toro Mijares, I., Vigneron, J.G., Barve, V., Dombrowik, V.L., Duong, M., Guralnick, R., Hart, J.A., Maypole, J.K., McCall, K., Ranipeta, A., Schuerkmann, A., Torselli, M.A., Lacher, T., Mittermeier, R.A., Rylands, A.B., Sechrest, W., Wilson, D.E., Abba, A.M., Aguirre, L. F., Arroyo-Cabrales, J., Astúa, D., Baker, A.M., Braulik, G., Braun, J.K., Brito, J., Busher, P.E., Burneo, S.F., Camacho, M.A., Cavallini, P., de Almeida Chiquito, E., Cook, J.A., Cserkész, T., Csorba, G., Cuéllar Soto, E., da Cunha Tavares, V., Davenport, T.R.B., Deméré, T., Denys, C., Dickman, C.R., Eldridge, M.D.B., Fernandez-Duque, E., Francis, C.M., Frankham, G., Franklin, W.L., Freitas, T., Friend, J.A., Gadsby, E.L., Garbino, G.S.T., Gaubert, P., Giannini, N., Giarla, T., Gilchrist, J.S., Gongora, J., Goodman, S.M., Gursky-Doyen, S., Hackländer, K., Hafner, M.S., Hawkins, M., Helgen, K.M., Heritage, S., Hinckley, A., Hintsche, S., Holden, M., Holekamp, K.E., Honeycutt, R.L., Huffman, B.A., Humle, T., Hutterer, R., Ibáñez Ulargui, C., Jackson, S.M., Janecka, J., Janecka, M., Jenkins, P., Juškaitis, R., Juste, J., Kays, R., Kilpatrick, C.W., Kingston, T., Koprowski, J.L., Kryštufek, B., Lavery, T., Lee, T.E., Leite, Y.R.L., Novaes, R.L.M., Lim, B.K., Lissovsky, A., López-Antoñanzas, R., López-Baucells, A., MacLeod, C.D., Maisels, F.G., Mares, M.A., Marsh, H., Mattioli, S., Meijaard, E., Monadjem, A., Morton, F.B., Musser, G., Nadler, T., Norris, R.W., Ojeda, A., Ordóñez-Garza, N., Pardiñas, U.F.J., Patterson, B. D., Pavan, A., Pennay, M., Pereira, C., Prado, J., Queiroz, H.L., Richardson, M., Riley, E.P., Rossiter, S.J., Rubenstein, D.I., Ruelas, D., Salazar-Bravo, J., Schai-Braun, S., Schank, C.J., Schwitzer, C., Sheeran, L.K., Shekelle, M., Shenbrot, G., Soisook, P., Solari, S., Southgate, R., Superina, M., Taber, A.B., Talebi, M., Taylor, P., Dinh, T.V., Ting, N., Tirira, D.G., Tsang, S., Turvey, S.T., Valdez, R., Van Cakenberghe, V., Veron, G., Wallis, J., Wells, R., Whittaker, D., Williamson, E.A., Wittemyer, G., Woinarski, J., Zinner, D., Upham, N.S., Jetz, W., 2022. Expert range maps of global mammal distributions harmonised to three taxonomic authorities. J. Biogeogr. 49 (5), 979–992.

Marshall, E., Wintle, B.A., Southwell, D., Kujala, H., 2020. What are we measuring? A review of metrics used to describe biodiversity in offsets exchanges. Biol. Conserv. 241, 108250.

Martínez-Fonseca, J.G., Westeen, E.P., Wan, H.Y., Cushman, S.A., Chambers, C.L., 2024. A global review of landscape-scale analyses in bats reveals geographic and taxonomic biases and opportunities for novel research. Biol. Conserv. 299, 110829.

Mascia, M.B., Pailler, S., Krithivasan, R., Roshchanka, V., Burns, D., Mlotha, M.J., Murray, D.R., Peng, N., 2014. Protected area downgrading, downsizing, and degazettement (PADDD) in africa, asia, and latin america and the caribbean, 1900-2010. Biol. Conserv. 169, 355–361.

Mazel, F., Guilhaumon, F., Mouquet, N., Devictor, V., Gravel, D., Renaud, J., Cianciaruso, M.V., Loyola, R., Diniz-Filho, J.A.F., Mouillot, D., Thuiller, W., 2014. Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. Glob. Ecol. Biogeogr. 23 (8), 836–847.

Mazel, F., Mooers, A.O., Riva, G.V.D., Pennell, M.W., 2017. Conserving phylogenetic diversity can be a poor strategy for conserving functional diversity. Syst. Biol. 66 (6), 1019–1027.

Mazel, F., Pennell, M.W., Cadotte, M.W., Diaz, S., Dalla Riva, G.V., Grenyer, R., Leprieur, F., Mooers, A.O., Mouillot, D., Tucker, C.M., Pearse, W.D., 2018. Prioritizing phylogenetic diversity captures functional diversity unreliably. Nat. Commun. 9 (1), 2888.

McKechnie, A.E., Rushworth, I.A., Myburgh, F., Cunningham, S.J., 2021. Mortality among birds and bats during an extreme heat event in eastern South Africa. Austral Ecol. 46 (4), 687–691.

Meyer, C., Kreft, H., Guralnick, R., Jetz, W., 2015. Global priorities for an effective information basis of biodiversity distributions. Nat. Commun. 6 (1), 1–8.

Mickleburgh, S., Waylen, K., Racey, P., 2009. Bats as bushmeat: a global review. Oryx 43 (2), 217–234.

Mikkonen, N., Moilanen, A., 2013. Identification of top priority areas and management landscapes from a national Natura 2000 network. Environ. Sci. Policy 27, 11–20.

Moilanen, A., Franco, A.M., Early, R.I., Fox, R., Wintle, B., Thomas, C.D., 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proc. R. Soc. B, Biol. Sci. 272, 1885–1891.

Moilanen, A., Kohonen, I., Lehtinen, P., Jalkanen, J., Virtanen, E., Kujala, H., 2022. Zonation 5 v1. 0 user manual.

Monadjem, A., Reside, A., 2008. The influence of riparian vegetation on the distribution and abundance of bats in an African savanna. Acta Chiropterologica 10 (2), 339–348.

Monadjem, A., Conenna, I., Taylor, P.J., Schoeman, M.C., 2018. Species richness patterns and functional traits of the bat fauna of arid southern Africa. Hystrix Italian J. Mammal. 29 (1), 19–24.

Monadjem, A., Healy, K., Guillerme, T., Kane, A., 2023. Dispersal ability is associated with contrasting patterns of beta diversity in African small mammal communities. J. Biogeogr. 50 (3), 539–550.

Monadjem, A., Montauban, C., Webala, P.W., Laverty, T.M., Bakwo-Fils, E.M., Torrent, L., Tanshi, I., Kane, A., Rutrough, A.L., Waldien, D.L., Taylor, P.J., 2024. African bat database: curated data of occurrences, distribution and conservation metrics for sub-Saharan bats. Sci. Data 11 (1), 1309.

Montauban, C., Budinski, I., Webala, P.W., Laverty, T.M., Tanshi, I., Torrent, L., Bakwo-Fils, E., Taylor, P.J., Kane, A., Monadjem, A., 2025. Underrepresentation of bats in africa's protected areas. Conserv. Biol., e70108

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403 (6772), 853–858.

Nori, J., Loyola, R., Villalobos, F., 2020. Priority areas for conservation of and research focused on terrestrial vertebrates. Conserv. Biol. 34 (5), 1281–1291.

O'Connor, L.M.J., Pollock, L.J., Renaud, J., Verhagen, W., Verburg, P.H., Lavorel, S., Maiorano, L., Thuiller, W., 2021. Balancing conservation priorities for nature and for people in europe. Science 372 (6544), 856–860.

Olival, K.J., Hosseini, P.R., Zambrana-Torrelio, C., Ross, N., Bogich, T.L., Daszak, P., 2017. Host and viral traits predict zoonotic spillover from mammals. Nature 546 (7660), 646–650.

Oliver, R.Y., Meyer, C., Ranipeta, A., Winner, K., Jetz, W., 2021. Global and national trends, gaps, and opportunities in documenting and monitoring species distributions. PLoS Biol. 19 (8), e3001336.

Patterson, B.D., Willig, M.R., Stevens, R.D., 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. In: Kunz, T.H., Fenton, M.B. (Eds.), Bat Ecology. University of Chicago Press, Chicago, pp. 536–579.

Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118 (3), 391–402.

Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5 (3), 402–411.

Pio, D.V., Engler, R., Linder, H.P., Monadjem, A., Cotterill, F.P.D., Taylor, P.J., Schoeman, M.C., Price, B.W., Villet, M.H., Eick, G., Salamin, N., Guisan, A., 2014. Climate change effects on animal and plant phylogenetic diversity in souther africa. Glob. Chang. Biol. 20 (5), 1538–1549.

Pipins, S., Baillie, J.E., Bowmer, A., Pollock, L.J., Owen, N., Gumbs, R., 2024. Advancing EDGE Zones to identify spatial conservation priorities of tetrapod evolutionary history. Nat. Commun. 15 (1), 7672.

Pollock, L.J., Rosauer, D.F., Thornhill, A.H., Kujala, H., Crisp, M.D., Miller, J.T., McCarthy, M.A., 2015. Phylogenetic diversity meets conservation policy: small areas are key to preserving eucalypt lineages. Philos. Trans. R. Soc., B 370 (1662), 20140007.

Pollock, L.J., Thuiller, W., Jetz, W., 2017. Large conservation gains possible for global biodiversity facets. Nature 546 (7656), 141–144.

Pollock, L.J., O'connor, L.M., Mokany, K., Rosauer, D.F., Talluto, M.V., Thuiller, W., 2020. Protecting biodiversity (in all its complexity): new models and methods. Trends Ecol. Evol. 35 (12), 1119–1128.

Popa-Lisseanu, A.G., Voigt, C.C., 2009. Bats on the move. J. Mammal. 90 (6), 1283–1289.

Pressey, R.L., Cowling, R.M., Rouget, M., 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. Biol. Conserv. 112 (1–2), 99–127.

Prieto-Torres, D.A., Rojas-Soto, O.R., Bonaccorso, E., Santiago-Alarcon, D., Navarro-Sigüenza, A.G., 2018. Distributional patterns of Neotropical seasonally dry forest birds: a biogeographical regionalization. Cladistics 35 (4), 446–460.

Pruvot, M., Cappelle, J., Furey, N., Hul, V., Heng, H.S., Duong, V., Dussart, P., Horwood, P., 2019. Extreme temperature event and mass mortality of insectivorous bats. Eur. J. Wildl. Res. 65 (3), 41.

Ralimanana, H., Perrigo, A.L., Smith, R.J., Borrell, J.S., Faurby, S., Rajaonah, M.T., Randriamboavonjy, T., Vorontsova, M.S., Cooke, R.S.C., Phelps, L.N., Sayol, F., Andela, N., Andermann, T., Andriamanohera, A.M., Andriambololonera, S., Bachman, S.P., Bacon, C.D., Baker, W.J., Belluardo, F., Birkinshaw, C., Cable, S., Canales, N.A., Carrillo, J.D., Clegg, R., Clubbe, C., Crottini, A., Damasco, G., Dhanda, S., Edler, D., Farooq, H., de Lima Ferreira, P., Fisher, B.L., Forest, F., Gardiner, L.M., Goodman, S.M., Grace, O.M., Guedes, T.B., Hackel, J., Henniges, M.C., Hill, R., Lehmann, C.E.R., Lowry, P.P., Marline, L., Matos-Maraví, P., Moat, J., Neves, B., Nogueira, M.G.C., Onstein, R.E., Papadopulos, A.S.T., Perez-Escobar, O.A., Phillipson, P.B., Pironon, S., Przelomska, N.A.S., Rabarimanarivo, M., Rabehevitra, D., Raharimampionona, J., Rajaonary, F., Rajaovelona, L.R., Rakotoarinivo, M., Rakotoarisoa, A.A., Rakotoarisoa, S.E., Rakotomalala, H.N., Rakotonasolo, F., Ralaiveloarisoa, B.A., Ramirez-Herranz, M., Randriamamonjy, J.E.N., Randrianasolo, V., Rasolohery, A., Ratsifandrihamanana, A.N., Ravololomanana, N., Razafiniary, V., Razanajatovo, H., Razanatsoa, E., Rivers, M., Silvestro, D., Testo, W., Torres Jiménez, M.F., Walker, K., Walker, B.E., Wilkin, P., Williams, J., Ziegler, T., Zizka, A., Antonelli, A., 2022. Madagasca's extraordinary biodiversity: threats and opportunities. Science 378 (6623), eadf1466.

Redford, K.H., 1992. The empty forest. BioScience 42 (6), 412–422.

Rocha-Ortega, M., Rodriguez, P., Córdoba-Aguilar, A., 2021. Geographical, temporal and taxonomic biases in insect GBIF data on biodiversity and extinction. Ecol. Entomol. 46 (4), 718–728.

Romanelli, C., Capon, A.G., Maiero, M., Campbell-Lendrum, D., Butler, C., Corvalan, C., Issa, R., McFarlane, R., von der Pahlen, C.T., 2015. Climate change, biodiversity and human health. In: Connecting Global Priorities: Biodiversity and Human Health.

Rosauer, D.F., Pollock, L.J., Linke, S., Jetz, W., 2017. Phylogenetically informed spatial planning is required to conserve the mammalian tree of life. Proc. R. Soc. B Biol. Sci. 284 (1865), 20170627.

Schoeman, M.C., Monadjem, A., 2018. Community structure of bats in the savannas of southern Africa: Influence of scale and human land use. Hystrix 29 (1), 3.

Schoeman, M.C., Cotterill, F.P.D., Taylor, P.J., Monadjem, A., 2013. Using potential distributions to explore environmental correlates of bat species richness in southern Africa: effects of model selection and taxonomy. Curr. Zool. 59 (3).

Šmíd, J., 2022. Geographic and taxonomic biases in the vertebrate tree of life. J. Biogeogr. 49 (12), 2120–2129.

Smith, A., Schoeman, M.C., Keith, M., Erasmus, B.F., Monadjem, A., Moilanen, A., Di Minin, E., 2016. Synergistic effects of climate and land-use change on representation of African bats in priority conservation areas. Ecol. Indic. 69, 276–283.

Tam, J., Lagisz, M., Cornwell, W., Nakagawa, S., 2022. Quantifying research interests in 7,521 mammalian species with h-index: a case study. Gigascience 11, giac074.

Tanshi, I., Obitte, B.C., Monadjem, A., Rossiter, S.J., Fisher-Phelps, M., Kingston, T., 2022. Multiple dimensions of biodiversity in paleotropical hotspots reveal comparable bat diversity. Biotropica 54 (5), 1205–1216.

Tattersall, I., 2009. Human origins: out of Africa. Proc. Natl. Acad. Sci. 106 (38), 16018–16021.

Thuiller, W., Maiorano, L., Mazel, F., Guilhaumon, F., Ficetola, G.F., Lavergne, S., Renaud, J., Roquet, C., Mouillot, D., 2015. Conserving the functional and phylogenetic trees of life of european tetrapods. Philos. Trans. R. Soc. B: Biol. Sci. 370 (1662), 20140005.

Titley, M.A., Snaddon, J.L., Turner, E.C., 2017. Scientific research on animal biodiversity is systematically biased towards vertebrates and temperate regions. PloS One 12 (12), e0189577.

Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., Legendre, F., 2017. Taxonomic bias in biodiversity data and societal preferences. Sci. Rep. 7, 9132.

UICN/PACO, 2009. La grande chasse en Afrique de l'Ouest: quelle contribution à la conservation? (Big Game Hunting in West Africa). What is its contribution to conservation?.

Upham, N.S., Esselstyn, J.A., Jetz, W., 2019. Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS Biol. 17 (12), e3000494.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116 (5), 882–892.

Wilson, D.E., Mittermeier, R.A. (Eds.), 2019. Handbook of the Mammals of the World, Vol. 9. Bats. Lynx Edicions, Barcelona.

Wood, S.N., 2006. Generalized Additive Models: An Introduction With R. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Woodley, S., Locke, H., Laffoley, D., MacKinnon, K., Sandwith, T., Smart, J., 2019. A review of evidence for area-based conservation targets for the post-2020 global biodiversity framework. Parks 25 (2), 31–46.

Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., Mouillot, D., Mouquet, N., Renaud, J., Thuiller, W., 2014. Spatial mismatch of phylogenetic diversity across three vertebrate groups and protecrted areas in europe. Divers. Distrib. 20 (6), 674–685.