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Biogeography of central African forests: Determinants, ongoing threats and conservation priorities of mammal assemblages

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Abstract

Aim: Central Africa shelters diverse and iconic megafauna, which is threatened by climate and land-use changes and increased hunting-induced defauna. Though crucial for coordinating regional conservation actions, how species assemblages are spatially structured remains poorly understood. This study aims to fill this knowledge gap for mammals across central African forests.

Location: Tropical moist forests from Nigeria to the Albertine Rift.

Methods: An extensive compilation of forest-dwelling mammal species lists was made from wildlife and bushmeat-related surveys across central Africa. A beta-diversity approach enabling the clustering of surveys composed of similar species was implemented to identify and delimit zoogeographic districts, separately for three well-documented mammal orders: carnivores, primates and artiodactyls. Random forest classification models were then used to identify the environmental determinants of the district's distribution and to produce a continuous zoogeographic map (and associated uncertainties) critical to assess the conservation status of each district and their ongoing threats.

Results: While carnivores do not present a clear spatial structure within central African forests, our findings highlight the structuring role of rivers on both primate and artiodactyl assemblages' distributions. We retained eight and six spatially congruent districts for primates and artiodactyls, respectively. These districts were shaped by the Ubangi-Congo River system, and the Cross and Sanaga Rivers, with a secondary role of insularity and precipitation identified for primates. Highly threatened districts were highlighted, especially in Nigeria and in the Democratic Republic of Congo, the latter including vast areas that are understudied and poorly represented in the protected area network.

Main Conclusions: Beyond refining our understanding of the diversity and uniqueness of mammalian assemblages across central African forests, our map of zoogeographic districts has far-reaching implications for the conservation of highly threatened taxa, allowing to target species and areas of interest for further sampling, conservation and rewilding efforts.

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KEYWORDS

artiodactyls, biogeography, carnivores, Central Africa, primates, rivers, terrestrial mammals, tropical forest

1 | INTRODUCTION

Within the Afrotropics, the Guineo-Congolian forest that stretches along west and central Africa is recognized as one of the four ecologically distinct continental-scale herbivory regimes, or herbivome (sensu Hempson et al., 2015), dominated by small, nonsocial browsers, including many duiker species. Within the Guineo-Congolian Region, central Africa represents the second largest block of continuous tropical forest after the Amazon and harbours some of the most iconic mammals in the world (Kreft & Jetz, 2010; Linder et al., 2012) such as forest elephants, gorillas, bonobos and okapis, among others. However, the entire region, which is a vast wilderness area (Mittermeier et al., 2003) and includes intact forest landscapes (Potapov et al., 2017), has never been recognized as a biodiversity hotspot (Ceballos & Ehrlich, 2006; Myers et al., 2000), even when refined for Africa (Küper et al., 2004), and remains largely understudied (Verbeeck et al., 2011). For example, new mammal species are still being discovered such as *Cercopithecus lomamiensis* in the most recent national park (NP) of the Democratic Republic of Congo (DRC), the Lomami NP (Hart et al., 2012). To date, the map of ecoregions (Dinerstein et al., 2017; Olson et al., 2001) represents the most detailed classification available for the region. However, this system is greatly inspired by White's phytochoria (White, 1983) and has never gone through a cross-taxa validation for mammals using data-driven approaches based on replicable quantitative methods such as multivariate statistics and clustering analyses (Kreft & Jetz, 2010).

While mammals are facing tremendous threats and environmental challenges across central Africa (Abernethy et al., 2016; Benítez-López et al., 2019; Bush et al., 2020; Grantham et al., 2020), we still lack a thorough understanding of how mammal assemblages are distributed across the region, though this knowledge is essential for planning coordinated conservation strategies and assessing where conservation gaps might persist. Historically, protected areas have been established in the region (i) to prevent excessive hunting and regulate recreational trophy hunting, (ii) to target emblematic species (e.g. the Okapi Wildlife Reserve in the DRC), (iii) to protect remarkable landscapes (e.g. the Mount Cameroon NP in Cameroon or the Virunga NP in the DRC) or (iv) for geopolitical reasons such as protected areas aligned along national borders (Doumenge et al., 2015). Where they existed, country-level conservation strategies were usually designed for protecting individual key areas and their surroundings. Currently, a few coordinated conservation actions at the regional scale have been promoted by international organizations, such as the USAID's CARPE program or the 'Larger than Elephant' (European Commission, Directorate-General for International Cooperation and Development, 2017) and the new 'Naturafrica' (European Commission, Directorate-General for International Partnerships, 2021) initiatives of the European Union.

The landscape approach they promote is based on networks of interconnected protected areas (transnationally or not), which aim to ensure ecological connectivity and maintenance of biodiversity at larger scales (e.g. protected areas in a matrix of forests dedicated to sustainable forest management). However, beyond the presence of emblematic species, it is the richness and uniqueness of species assemblages that primarily determines the conservation value of an area and, in most cases, this component has been neglected or only studied retroactively after the creation of the protected areas.

In this study, we fill a critical knowledge gap concerning biogeographic patterns and determinants of mammal assemblages across central African forests and we outline the implications for biodiversity conservation in the region. Specifically, we used a standardized analytical road map based on (dis)similarity in species composition (Kreft & Jetz, 2010) to delineate zoogeographic districts at a scale suitable for the regional management of conservation actions and investments (Wyborn & Evans, 2021), i.e. the COMIFAC ('Commission des Forêts d'Afrique Centrale') working scale. To do so, we gathered species lists from wildlife and bushmeat-related surveys focusing on medium-sized to large mammals. The combined dataset includes 6840 occurrences across central Africa (Figure 1) for 31 species of carnivores (out of 35 species in the study area according to Wilson & Mittermeier, 2009), 64 species of primates (out of 73 according to Mittermeier et al., 2013) and 49 species of artiodactyls (out of 57 according to Wilson & Mittermeier, 2011). Beyond investigating how mammal assemblages are distributed, we also estimate their uniqueness across the region (assessing the indicator value of the species they hold), how well they are represented in the conservation network (assessing the protected area coverage) and the threats they face (assessing hunting-induced defaunation and loss of forest integrity). We specifically sought to address the following questions:

1. Is variation in mammal assemblages congruent across taxonomic orders? While few studies examined the biogeography of very specific groups (herpetofauna by Chifundera, 2019; primates by Colyn et al., 1991; guenons by Colyn & Deleporte, 2004; and birds by De Klerk et al., 2002), the distribution and diversity of mammal assemblages across central African forests remain poorly understood.
2. What are the environmental and spatial determinants that shape the distribution of mammal assemblages? Previous studies have highlighted the role of river networks (Aliaga-Samanez et al., 2020; Oliveira et al., 2017), mountain ranges and insular isolation (Fa & Funk, 2007) as important determinants of species distribution and species assemblages worldwide. However, the role of these determinants across central African forests has yet to be verified.

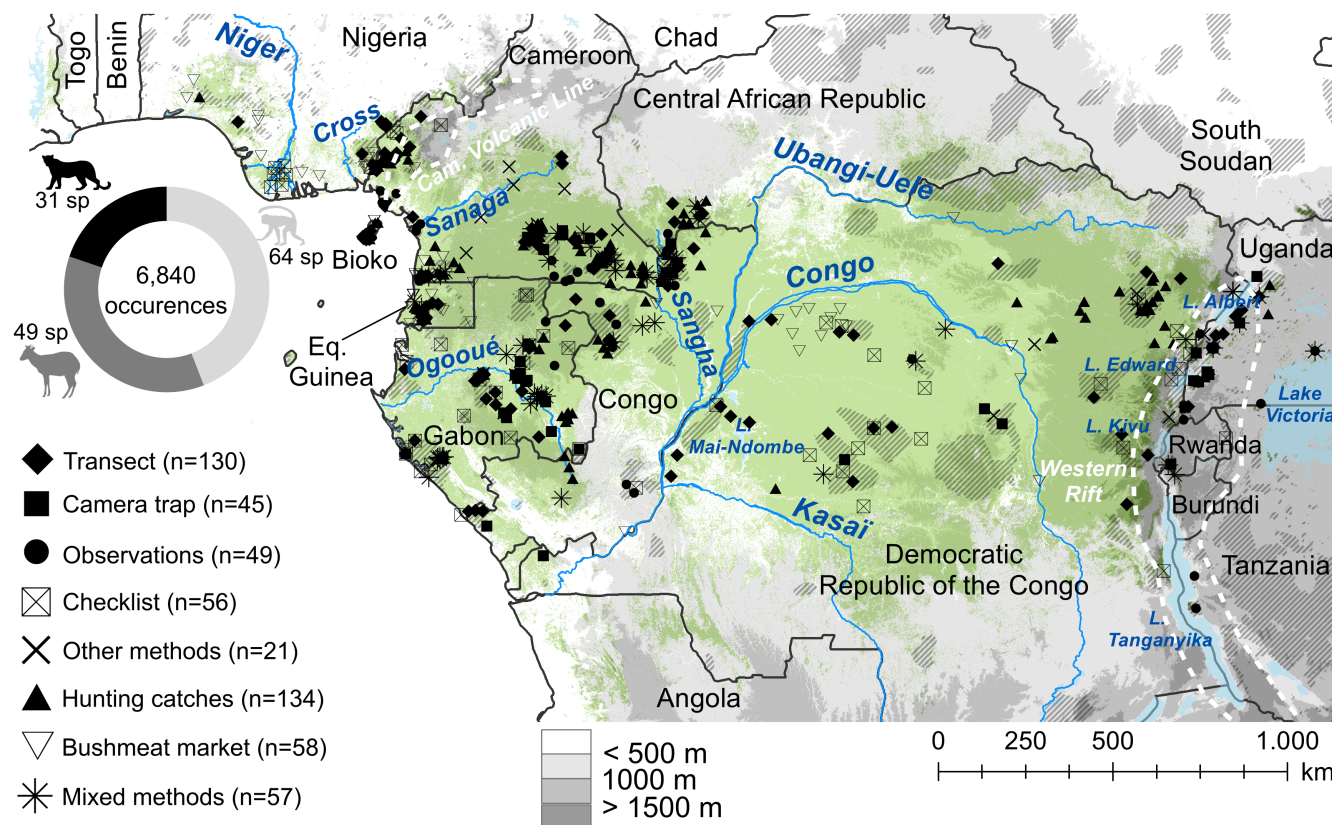


FIGURE 1 Location of the mammal species lists. Species lists were retrieved from wildlife surveys (transects, camera traps, observations, checklists and other methods) and bushmeat-related surveys (hunting catches and bushmeat market records), and a mix of the two. The eight major rivers (in blue) and the two mountain chains (in white, dotted lines) are considered potential biogeographical barriers. The distribution of the moist forest (in green) is derived from the Copernicus Global Land Cover classification (Buchhorn et al., 2020). Hatched areas correspond to protected areas (IUCN & UNEP-WCMC, 2018). The background map corresponds to the altitude (greyscale) retrieved from the Shuttle Radar Topography Mission (Jarvis et al., 2008). The pie chart provided as an inset shows the proportion and the number of species of each order in the dataset. Animal silhouettes were provided with courtesy of PhyloPic (www.phylopic.org) or adapted from Wilson and Mittermeier (2011).

3. What is the overall conservation status of the region and which assemblages are the most threatened and the least protected? We thus investigate how well each zoogeographic district is protected by the existing protected area network and the level of anthropogenic threat each district faces.

2 | METHODS

2.1 | Species lists and taxonomy standardization

We gathered mammal species lists from 550 surveys conducted in the lowland forests of central Africa and in the mountain forests of the Albertine rift (Figure 1). This dataset constitutes an original contribution (<https://doi.org/10.5061/dryad.qjq2bvqkb>) and has never been published before. Importantly, it aggregates much-needed information for conservation from a highly diverse yet data-deficient region. Our study area matches the distribution of the moist forest biome in central Africa derived from the Copernicus Global Land Cover classification (Buchhorn et al., 2020) and encompasses

the following countries: Nigeria, Cameroon, Equatorial Guinea (Rio Muni and Bioko Island), Gabon, Republic of Congo, Central African Republic, Democratic Republic of Congo, Uganda, Rwanda, Burundi and Tanzania (Figure 1). We pulled together mammal species lists gathered from wildlife (e.g. camera trap surveys, line transects) and bushmeat-related (e.g. hunting bag data from rural villages, stalls in bushmeat markets) surveys including the grey literature (e.g. monitoring reports made in protected areas). We first employed a systematic search on Google Scholar by using keywords related to the taxonomic groups studied (mammals and specific orders within mammals), the study area (central Africa, Congo basin and individual country names), the survey methods (line transect, camera trap, bushmeat or hunting study), and we also included surveys suggested by collaborators, fellow researchers and conservation practitioners. We only included surveys providing evidence of species occurrence (e.g. direct observations, hunting catches and DNA samples). Surveys conducted in the same area by different researchers and/or during different seasons or years were considered independently. A single location was given for surveys covering a wide area (e.g. multiple line transects or camera trap grids) or a whole protected area (e.g.

checklist for an entire national park), and in these cases, we chose the centroid. We recognized that the assembled species lists do not come from studies with similar objectives and similar methodologies, as shown in the detailed metadata provided with the dataset. Hunting studies, for example, only record species sought for the bushmeat trade and do not necessarily reflect the whole mammalian community within a site. Since the surveys span a vast period, from 1932 to 2019, some species assemblages reported here might have already been altered or completely extirpated due to hunting or habitat destruction. Also, since we have included surveys from forest-savanna mosaics, a few savanna taxa are present in our combined dataset. Savanna taxa were not removed as forest-savanna mosaics are common in central Africa (e.g. Lopé NP in Gabon, Odzala-Kokoua NP in the Republic of Congo) and might potentially display unique assemblages. Furthermore, the attribution of unique habitats to species remains subjective, especially for generalist species such as the leopard (*Panthera pardus*) or the chimpanzee (*Pan troglodytes*) that can occur in both forests and savannas.

When assembling data from vastly different collection methods and sources, data-cleaning procedures are necessary; the approach we implemented is detailed below. Similar practices are needed when dealing with big data repositories such as the Global Biodiversity Information Facility (GBIF, www.gbif.org), which compiles valuable data for research (Zizka et al., 2020) and have revolutionized scientific biogeography (Edler et al., 2016). Rather than occurrence data of individual species, we assembled species lists reflecting coexisting species. We focused our analyses of species assemblages on carnivores, primates and artiodactyls for two reasons. First, these three orders are well-documented across the region, with 307, 514 and 386 surveys, respectively. Second, identification at the species level for these three orders is more reliable and less prone to identification errors, contrary to rodents for instance, which pose important identification challenges. Original species identifications were deemed correct, and taxonomy was standardized and updated according to Mittermeier et al. (2013) and Wilson and Mittermeier (2009, 2011). In a few cases, the new taxonomic status led to a change in the species distribution range. We encountered this situation for one carnivore species, 12 primate species and 19 artiodactyl species. For instance, the blue duiker, which was previously described as one species—*Cephalophus monticola*—is now divided into five different species in the study area, *Philantomba melanorhea*, *P. congica*, *P. simpsonii*, *P. anchietae* and *P. aequatorialis*. As we assembled surveys from different sources, including species identifications from nonzoological experts, we also discarded unreliable records (i.e. outside the known range of the species) at this stage, which corresponded to 6.5% of occurrences for carnivores, 4.6% for primates and 2.5% for artiodactyls, respectively.

2.2 | Zoogeographic districts and indicator species

All analyses were performed in R 3.6.3 (R Core Team, 2019). After the data checking and cleaning procedure, we applied a

dissimilarity-based approach adapted to heterogeneous data of species composition. First, we quantified dissimilarity in species composition between each pair of surveys using the Simpson beta-diversity index, which is known to be richness-independent (Koleff et al., 2003). This index ranges between 0 (similar species composition between two surveys) and 1 (no shared species) and is suited to presence-only data and unbalanced sampling (Kreft & Jetz, 2010; Linder et al., 2012). To account for artefacts due to rarity, we removed the species present in less than three surveys and the surveys recording less than three species, a standard practice in community analyses (Couteron et al., 2003). We used the *vegan* package (Oksanen et al., 2019) to compute the pairwise dissimilarity matrices for carnivores, primates and artiodactyls. Afterward, we clustered all surveys according to their mammal species composition by applying Ward's hierarchical classification algorithm on the three dissimilarity matrices. To divide the resulting classification into meaningful zoogeographic districts, we established three criteria: (1) district average silhouette width, (2) district number of indicator species and (3) spatially coherent district distribution. We investigated all possible geographic divisions up to a maximum of 10 potential clusters per order. We calculated silhouette values by using the *cluster* package (Maechler et al., 2019). Silhouette scores range from −1 to 1 and indicate how strongly a given survey is associated with its cluster. Negative values indicate a poor assignment—the survey being on average closer to surveys in another cluster than to surveys of its own cluster. To detect the significant indicator species of each cluster or combination of clusters, we calculated the indicator value (*indval*) with the *multipatt* function of the *indicspecies* package (De Cáceres & Legendre, 2009). *indval* is based on two components, species specificity and fidelity (De Cáceres, 2020). Since species detectability cannot be considered equal between different survey methods, we only considered the specificity component, which is the probability that the survey belongs to the target cluster given the fact that the species has been found. Species specificity ranges from 0 (no association with the district) to 1 (full association with the district). Finally, from these clusters, we retained and labelled a set of zoogeographic districts that show a coherent spatial distribution and a particular species composition.

After identifying the different zoogeographical districts for each order, we checked whether data heterogeneity and species sampling incompleteness might have influenced the identification of our districts. First, we used an ordination (Nonmetric Multidimensional Scaling) for visualization of data heterogeneity and tested for significant differences between survey methods, survey headcount, year of data collection and survey duration with a series of analyses of similarity (ANOSIM). We also used the *vegan* package (Oksanen et al., 2019) for these analyses. Second, we explored the issues of incompleteness and bias in species sampling (e.g. lack of nongame species in bushmeat surveys, lack of arboreal species in ground camera trap surveys). To do so, we built a presence matrix for each order by intersecting over a 0.1° grid all IUCN species range maps, i.e. an expert-based delineation of the species distribution also potentially biased and provided at a lower taxonomical resolution, and

then applied the same methodological road map for delineating zoogeographic districts on these virtual species assemblages (Kreft & Jetz, 2010; Linder et al., 2012).

2.3 | Determinants and coverage of the districts

We tested the relative importance of climate (temperature and precipitation), forest structure (tree cover), rivers (riverbank side), insularity (Bioko vs continent) and elevation in structuring central African forests' mammal species assemblages. We retrieved values of annual mean, minimum and maximum temperature (Bio1, Bio5 and Bio6) and precipitation (Bio12, Bio13 and Bio14), and the precipitation variation coefficient (Bio15), from the 'WorldClim 2' Global Climate database (Fick & Hijmans, 2017) at a 30 arc-second resolution. We assessed forest structure by relying on the percentage of tree cover (Hansen et al., 2013). We also tested whether the river network acts as a driver of mammal species assemblages. To this end, we focused on the seven main rivers present in the region (Figure 1, the Kasai River was not tested because of the lack of surveys on its left bank), and for each river, we built a categorical variable to describe whether a survey was carried out on its right bank, left bank or upstream of the river source. We also tested the importance of elevation and insularity for explaining the regional patterns of mammal assemblages. Elevation data were extracted from the CGIAR-CSI SRTM 90m database (Jarvis et al., 2008) and, for insularity, we created a categorical variable indicating whether surveys are located on Bioko Island or on the continent. To determine the importance of environmental and spatial determinants and to predict the coverage of each district at the regional scale, we used a random forest classification model approach that is particularly suited when predictors are a mix of continuous and categorical variables (Strobl et al., 2009). Specifically, we trained 100 random forest classification models (with 1000 unbiased individual trees to grow in each model) for each order separately using the *party* package (Strobl et al., 2007). The model training was done on a calibration dataset composed of surveys strongly associated with their district (with a silhouette score > 0.2). Since the number of surveys for each district was unevenly distributed, which can cause model overfitting towards the best-represented classes, we built our random forest models by allowing survey sampling with replacement (a single survey can be sampled more than once), a robust and suitable technique for handling class imbalance (Gosain & Sardana, 2017). We did this until all districts had the same number of surveys present in the best-sampled district. By doing so, we achieved sampling evenness for all districts ($n = 90$ for primates, $n = 147$ for artiodactyls). We estimated model accuracy by assessing the out-of-bag error, which corresponds to the prediction error of the model obtained through a bootstrap aggregating technique. The importance of each predictor was assessed by testing how the accuracy of the results was affected when the predictor variable was randomly permuted (function *varimp* of the same package). We modelled the districts' spatial distribution and associated prediction uncertainty at 0.1° grid resolution throughout the whole extent of the

evergreen broadleaved forests (Buchhorn et al., 2020). We mapped the modelled districts by plotting the most frequently predicted district category for each pixel out of the 100 models built.

2.4 | Conservation status and anthropogenic threats

To estimate the conservation status of each district and the level of anthropogenic threat they face, we gathered information on protected area coverage (Figure 1) and human-induced pressures. We retrieved the protected area network from the World Database on protected areas (IUCN & UNEP-WCMC, 2018). We only considered nationally recognized protected areas with a designated or inscribed status (Grantham et al., 2020) and excluded aquatic reserves and marine parks. We considered two anthropogenic threats, a defaunation index (DI), corresponding to the estimated hunting-induced reduction in mammal abundance (Benítez-López et al., 2019), and a Forest Landscape Integrity index (FLI), which integrates the observed and inferred human pressure associated to infrastructure, agriculture, recent deforestation and loss of forest connectivity (Grantham et al., 2020). The DI index is a composite index equal to the minimum value between the original DI index for medium (1–20 kg) mammal species and the original DI index for large (>20 kg) mammal species (Benítez-López et al., 2019). To ease the comparison among districts, DI and FLI were both rescaled between 0 and 1. We then produced a synthetic map summarizing both threats in the study area categorizing each pixel as 'highly', 'moderately' and 'weakly' impacted according to the thresholds proposed in the original studies.

3 | RESULTS

3.1 | Congruence of biogeographic patterns across primates and artiodactyls

Carnivores did not exhibit a clear spatial structure across central African forests, and we ended up with a broad and unique Congolian district with no further spatially relevant divisions since the average silhouette values were consistently low starting from the first division (Appendix S1, Figure S1.1). By contrast, species assemblages for primates and artiodactyls displayed refined and highly congruent distribution patterns. After the first split, separating surveys conducted on the eastern and western sides of the Ubangi-Congo River system, we retained nine clusters for primates and seven clusters for artiodactyls, which were supported by high silhouette values and many indicator species (Appendix S1, Figure S1.1). Based on clusters' spatial coherence and species composition, we finally identified eight districts for primates and six districts for artiodactyls across central African forests (Figure 2). From west to east, the following six districts were common to the two orders: 'South Nigeria', 'Cameroonian Highlands', 'Inland' in Atlantic central Africa,

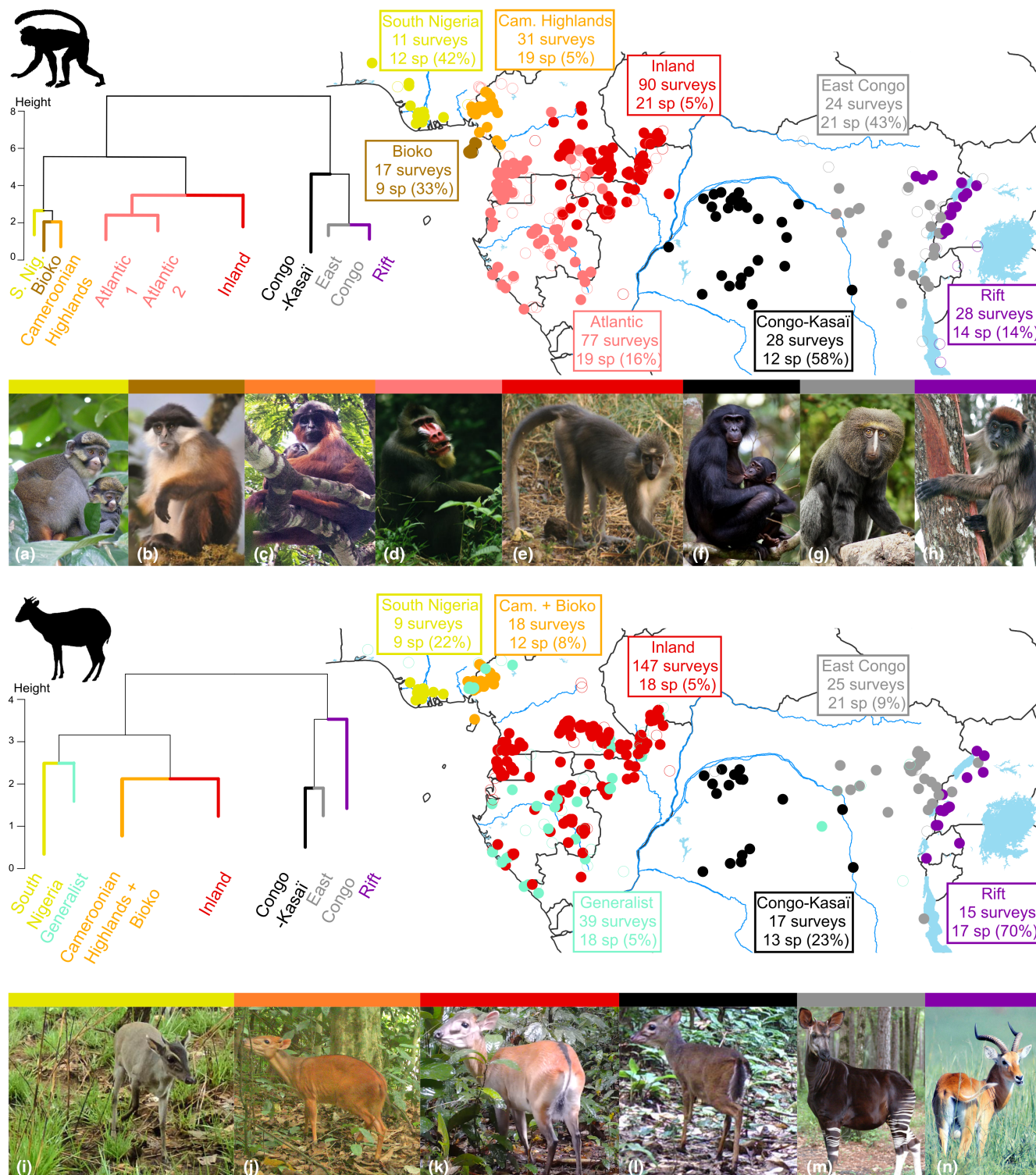


FIGURE 2 Zoogeographical districts for primates and artiodactyls across central African forests. The dendrograms (Ward's algorithm on Simpson dissimilarity) show the relatedness between districts that are also displayed on the map. Filled and empty circles, respectively, correspond to silhouette scores greater and lower than 0.2. The species pool, the proportion of indicator species (considering strict indicators, not in combination with other districts) and the number of surveys (with a silhouette score > 0.2) are given for each district. Animal photographs display important indicator species of each district, following the same colour scheme. Species name and photo courtesy are given for primates, *Cercopithecus sclateri* (a) by Lynne R. Baker, *Ptilocolobus pennantii* (b) by Richard A. Bergl, *Ptilocolobus preussi* (c) by A. N. Hofner, *Mandrillus sphinx* (d) and *Cercocebus agilis* (e) by Brent Huffman/UltimateUngulate, *Pan paniscus* (f) by Takeshi Furuichi, *Cercopithecus hamlyni* (g) by Paul Moine, *Ptilocolobus tephrosceles* (h) by Thomas T. Struhsaker; and for artiodactyls, *Philantomba walteri* (i) by Délagnon Assou, *Cephalophus ogilbyi* (j) by WCS Nigeria, *Cephalophus leucogaster* (k) by Davy Fonteyn, *Philantomba simpsoni* (l) by John Hart/Frankfurt Zoological Society TL2 Project, *Okapia johnstoni* (m) by Bob Jenkins and *Kobus thomasi* (n) by Giuseppe Mazza.

'Congo-Kasai', 'East Congo' and a last district corresponding to the 'Rift'. For primates, Bioko Island formed a distinct 'Bioko' district from that of the 'Cameroonian Highlands', and an 'Atlantic' district extending along the coast of Cameroon and Rio Muni and deeper inland in Gabon was identified. This 'Atlantic' district was formed by the combination of two clusters (two branches in the dendrogram, Figure 2), and among them, the 'Atlantic 2' cluster was composed of several surveys with low silhouette values (mean silhouette value of -0.04 , Appendix S1, Figure S1.1) indicating a transitional composition (empty circles on Figure 2). While no species typified these two clusters individually, three species were identified as significant indicators when considering them combined in the 'Atlantic' district. For artiodactyls, a 'generalist' cluster was also identified but not recognized as a separate zoogeographic district because of its diffuse spatial distribution (Figure 2), the very low silhouette value (Appendix S1, Figure S1.1) and a nonspecific composition dominated by species vastly distributed in the study area (Appendix S1, Table S1.1).

The proportion of indicator species varied greatly among orders (Figure 2). Primates usually presented more endemic assemblages with 78% of the species ($n = 50$ out of 64) being significant indicators of at least one district. The proportion of indicator species also varied between districts with some districts being characterized by particularly unique mammal assemblages (Figure 2, Appendix S1, Table S1.1). For instance, more than half (58%) of the primate species occurring in the 'Congo-Kasai' district were strictly associated with this district, the Bonobo (*Pan paniscus*) being one of the most typical examples. With 42% and 33% of indicator species, respectively, 'South Nigeria' and 'Bioko' also presented unique but species-poor primate assemblages. In contrast to primates, only a few artiodactyl species ($n = 33$ out of 49) were identified as significant indicators (Appendix S1, Table S1.1). Only one species strictly typified the 'Cameroonian Highlands' (*Cephalophus ogilbyi*) and the 'Inland' (*Cephalophus leucogaster*) districts and the 'generalist' cluster mentioned above (the generalist *Syncerus nanus*, with a very low species specificity = 0.53). By contrast, the 'Rift' district showed a highly specific assemblage with 70% of artiodactyl species being significant indicators (Appendix S1, Table S1.1). However, some of these species are widespread across Africa such as the savanna buffalo (*Syncerus caffer*) and would not be indicators of the Rift in a larger analysis considering the full species range.

Then, we checked whether data heterogeneity and species sampling incompleteness might have influenced our classification of districts. First, we found only limited influence of surveys characteristics (method, headcount, year and duration) on the (dis)similarity in species composition separately for primates and for artiodactyls, the value of all ANOSIM tests remaining very low ($R < 0.21$, Appendix S1, Figure S1.2). By contrast, we found a strong and significant dissimilarity among districts (ANOSIM statistics close to 1, $R = 0.782^{**}$ for primates and $R = 0.669^{**}$ for artiodactyls) that were well discriminated on the ordination (NMDS). Second, the zoogeographical patterns and the associated discontinuities obtained by the IUCN-based analysis largely matched our district classification.

The Ubangi-Congo River system emerged quickly in the hierarchical clustering, at $k = 3$ for both primates and artiodactyls and at $k = 2$ for carnivores. For primates, the IUCN-based clusters were highly congruent with our classification, and most primate districts were retrieved at $k = 7$, with, however, two new districts in the DRC, in areas poorly sampled by ground surveys: the southern part of the Congo-Kasai interfluvium and a vast eastern area covering the Maniema, and the North and South Kivu provinces (Appendix S2, Figure S2.1). For artiodactyls, despite the East-West dichotomy, the lack of congruence between the two data sources (ground surveys vs IUCN range maps) likely reflects the lower resolution of the IUCN taxonomy.

3.2 | Determinants and coverage of primate and artiodactyl assemblages

We identified the environmental and spatial determinants driving the district distribution with a random forest approach employed on the 306 primate surveys (73% of the dataset) and the 270 artiodactyls surveys (82% of the dataset) well typifying the districts (with a silhouette value > 0.2 , filled circles on Figure 2). Our classification models were highly precise (out of bag error = 4.8% for primates, 1.7% for artiodactyls) and showed the leading role of rivers, specifically the Ubangi, Sanaga, Cross and Congo Rivers, in structuring primate and artiodactyl assemblages across central African forests (insets in Figure 3). For primates, insularity (separating Bioko's assemblage from those found on the continent) and precipitation-related variables (Bio12, 15 and 13) were also found to be important determinants. The latter discriminated the wetter and less seasonal forests of the 'Atlantic' district from that of the drier and more seasonal 'Inland' district (Figure 3), though we detected an important introgression between these two districts located near the north-eastern border of Gabon, and north of the Dja Faunal Reserve in Cameroon and perhaps up to the surroundings of Yaoundé (Figure 2).

Using our random forest classification models, we further predicted the distribution of the zoogeographical districts and the associated uncertainties (Figure 3). The 'South Nigeria', 'Rift' and to a lesser extent the 'Cameroonian Highlands' appeared restricted in terms of spatial coverage (Table 1) and highly fragmented (Figure 3). The spatial predictions of the 'Rift' district notably differ between primates and artiodactyls (Table 1, Figure 3) because of a few primate surveys in the lowlands and foothills that were included in this district (Figure 2). By contrast, the 'Inland' district in Atlantic central Africa and the 'Congo-Kasai' and 'East Congo' districts in the Congo basin covered more than 500,000 km² each (Table 1). The spatial extent of the 'East Congo' district, however, remains to be evaluated with ground data since an immense area between the Ubangi and Congo Rivers did not contain any ground surveys, as reflected by the weak prediction of the model (Figure 2) and part of this area corresponds to the central Congo Basin peatland complex. Also, it is worth reminding that the mammal assemblage may not be as rich and diverse across all the districts' areas because of local threats to biodiversity.

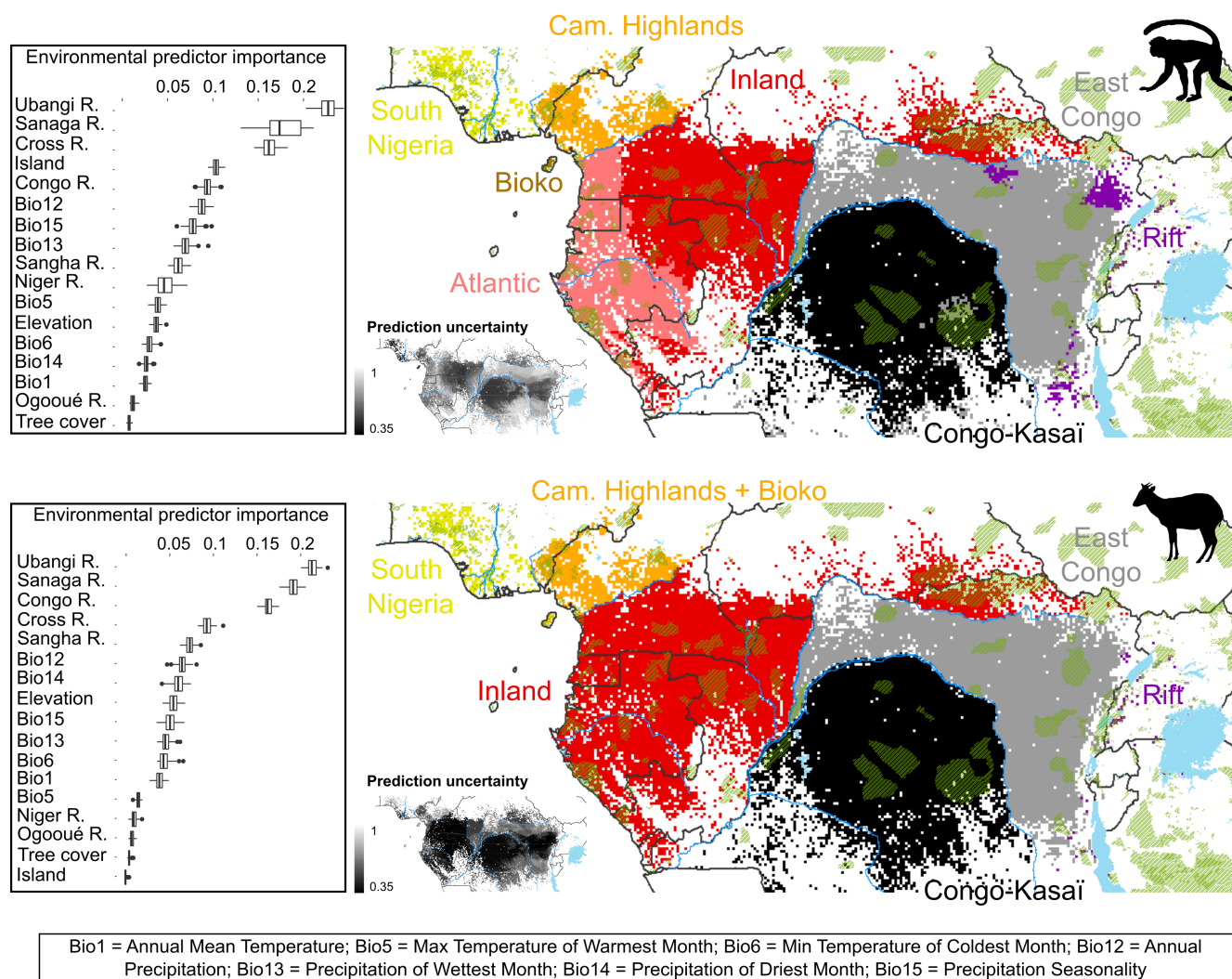


FIGURE 3 Environmental and spatial determinants and predicted distribution with associated uncertainties of the zoogeographical districts identified for primates and artiodactyls across central African forests. The importance of environmental and spatial predictors in the random forest classification models corresponds to the mean decrease in the accuracy of the prediction when the predictor variable is randomly permuted in the training dataset. Each 0.1° pixel across the moist forest area derived from the Copernicus Global Land Cover classification (Buchhorn et al., 2020) is assigned to the most frequently predicted district by 100 random forest classification models (see Figure 2 for the district colour scheme). The green hatched areas indicate the protected area network (IUCN & UNEP-WCMC, 2018).

3.3 | Conservation status and level of threats

We further assessed the protected area coverage on the predicted distribution of the zoogeographical districts (Figure 3) and the levels of ongoing threats across the region (Figure 4), using existing maps of hunting-induced defauna (Benítez-López et al., 2019) and forest integrity (Grantham et al., 2020). We found that the proportion of protected areas ranged between 11% and 67% among districts (Table 1). The 'Congo-Kasai' and 'East Congo' districts in the DRC are the least protected, with only 12% and 11% of their area in protected areas. It is worth noting that this protection level is relative to the current forest area and can be high and misleading for districts presenting small, protected patches of remnant forests, such as the 'South Nigeria' and the 'Rift', and to a lesser

extent, the 'Cameroonian Highlands'. The levels of ongoing threats vary across central African forests, and we detected scattered hot-spots of anthropogenic threats and very few undisturbed areas (Figure 4). The unique 'South Nigeria' mammal assemblage is by far the most threatened district with high defauna (mean defauna of the district, $DI = 0.16$) and poor forest integrity ($FI = 0.44$) even though 17% of its forests are protected (Table 1). While relatively well protected (20%–63%), the 'Rift' district also experiences a high level of threats (Figure 4). Defauna is also significant in the 'Cameroonian Highlands' and 'Bioko' districts though forest integrity appeared relatively high. The largest districts, 'Inland' (and 'Atlantic' for primates), 'Congo-Kasai' and 'East Congo', appear less threatened, with vast areas in and near protected areas with low defauna and high forest integrity.

Order	District	Total area in km ² (proportion in protected area, in %)	\overline{DI}	\overline{FLI}
Primates	South Nigeria	40,740 (16.2)	0.16	0.44
	Cameroonian Highlands	83,577 (17)	0.24	0.79
	Bioko	1474 (66.7)	0.53	0.62
	Atlantic	231,991 (13.1)	0.47	0.81
	Inland	539,904 (18.2)	0.59	0.88
	Congo-Kasaï	614,250 (12.2)	0.61	0.76
	East Congo	551,356 (11.7)	0.60	0.74
	Rift	41,789 (19.7)	0.55	0.75
Artiodactyls	South Nigeria	41,355 (17.8)	0.17	0.45
	Cameroonian High. + Bioko	84,436 (17.1)	0.24	0.79
	Inland	771,895 (16.7)	0.55	0.85
	Congo-Kasaï	649,928 (12.4)	0.61	0.75
	East Congo	550,580 (11.6)	0.60	0.75
	Rift	6886 (62.5)	0.37	0.53

Note: Total coverage and proportion of areas under protection status, mean defaunation index (\overline{DI}) (0 virtually represents a completely defaunated mammal community and 1 an intact community; Benítez-López et al., 2019) and mean forest landscape integrity index (\overline{FLI}) ranging from no forest integrity (0) up to complete forest integrity (1) (Grantham et al., 2020) are provided for each zoogeographical district.

4 | DISCUSSION

In this study, we aimed to describe the distribution and diversity of mammal assemblages across central African forests, which is critical information for the development of adapted conservation strategies at the regional scale. Covering a broad range of taxa, we refined previous zonations of primate communities in the Congo basin (Colyn et al., 1991; Colyn & Deleporte, 2004; Gautier-Hion et al., 1999) and herbivore communities across the African continent (Hempson et al., 2015). First, we found that carnivores form a broad and unique Congolian district. The lack of spatial structure reflects the wide distribution of most carnivore species in central Africa (e.g. *Caracal aurata*, Bahaa-el-din et al., 2015) and their ecology, being highly mobile and having broad habitat and dietary niches (Wilson & Mittermeier, 2009) like their Neotropical relatives (Cruz et al., 2022). By contrast, we found highly congruent spatial patterns for primate and artiodactyl assemblages across central African forests. Our dissimilarity-based approach applied to a newly assembled dataset from a data-deficient region (Siddig, 2019; Verbeeck et al., 2011) identified six common districts including from west to east, 'South Nigeria', 'Cameroonian Highlands' (for primates—'Cameroonian Highlands' and 'Bioko'), 'Inland' in Atlantic central Africa (for primates—'Inland' and 'Atlantic'), 'Congo-Kasaï', 'East Congo' and the 'Rift'. The highly fragmented 'South Nigeria' district presents unique but species-poor assemblages, notably for primates, probably due to long-lasting anthropogenic pressure in the region that had already led to a reduced diversity before the first studies were conducted (species list only available after

TABLE 1 Conservation status and anthropogenic threats faced by the zoogeographical districts.

1980). Nigeria is by now the most populous country in sub-Saharan Africa (Vollset et al., 2020) and has been significantly impacted by human activities (Venter et al., 2016), particularly by high volumes of bushmeat extraction from remnant forests (Fa et al., 2006). For the 'Bioko' district, the thriving primate-oriented bushmeat trade (Cronin et al., 2017) has undoubtedly put additional pressure on an already species-poor primate assemblage, since the island has gone through an extinction debt since its separation from the African continent 10,000–14,000 years ago (Jones, 1994). Though highly fragmented, the 'Rift' district showed a highly specific assemblage, notably for artiodactyls, revealing the richness and uniqueness found at the boundary of the forest and savanna biomes. This area is also a particular biogeographical unit for birds (De Klerk et al., 2002), amphibians and reptiles (Chifundera, 2019), and a regional mosaic for plants (White, 1983). However, artiodactyls and primates show less congruent spatial patterns in the 'Rift' district, probably because most primates are confined to the forest habitat while many artiodactyl species occurring in this district (including indicator species) are savanna species. Within the lowland tropical forests of DRC, we identified a range of primate and artiodactyl species, besides the flagship species like the bonobo and the okapi, that make the 'Congo-Kasaï' and 'East Congo' districts particularly unique. By contrast, the 'Cameroonian Highlands' and 'Inland' districts, and 'Atlantic' for primates, exhibit rich species assemblages but are mostly composed of widely distributed species with low indicator value (Appendix S1, Table S1.1) such as the putty-nosed monkey (*Cercopithecus nictitans*) or the red river hog (*Potamochoerus porcus*).

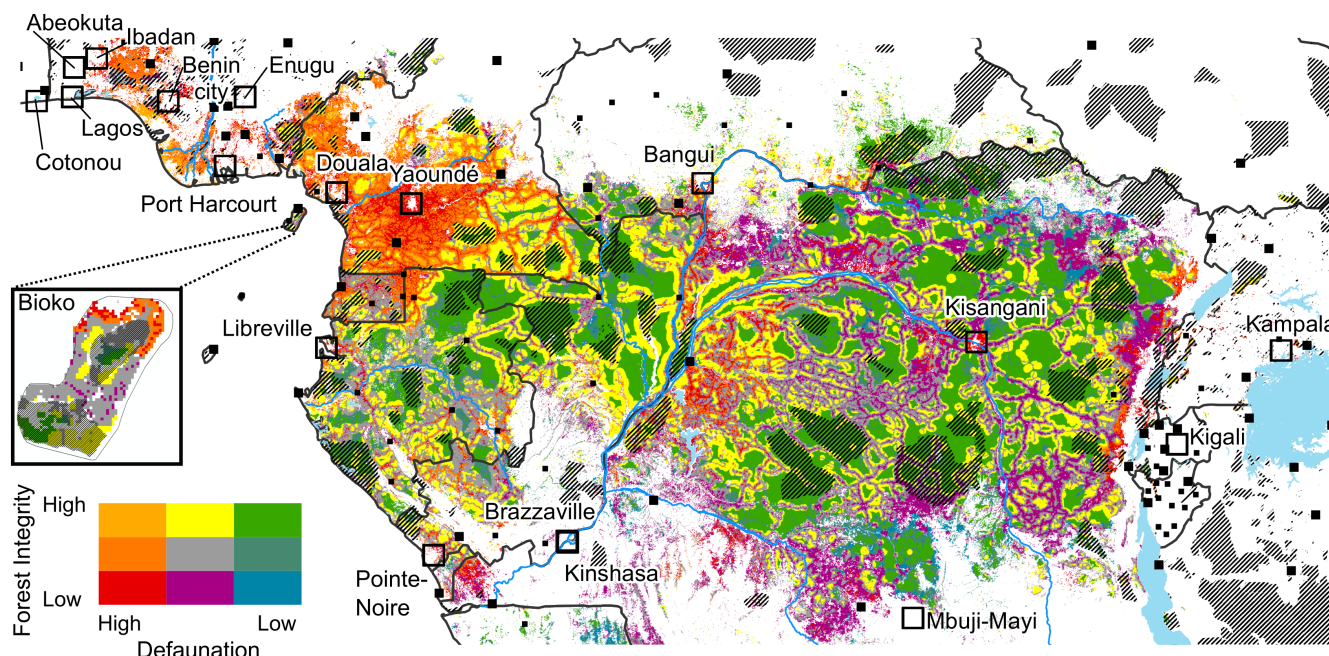


FIGURE 4 Synthetic map of anthropogenic threats across central African forests, combining the levels of defaunation (Benítez-López et al., 2019) and forest integrity (Grantham et al., 2020). Each pixel is coloured according to the level of pressure it faces ranging from red 'highly defaunated and a low forest integrity' to green 'nearly intact mammal community and a high forest integrity'. The colour code for intermediate pressure levels is presented in the inset. A zoom on Bioko Island is also displayed as an inset. Major urban centres (>500,000 inhabitants), cities (50,000–500,000 inhabitants) and towns (less than 50,000 inhabitants) according to the World Cities layer by ESRI (<http://www.arcgis.com>, Esri, DeLorme Publishing Company) are represented by black squares with a decreasing size according to the city population. The black-hatched areas represent the protected area network (IUCN & UNEP-WCMC, 2018).

The Ubangi-Congo River system was found to be an important discontinuity, driving the first split in the clustering for both primate and artiodactyl assemblages, and this result was also supported by the IUCN-based analysis for the three orders, including carnivores (Appendix S2, Figure S2.1). It is also an important discontinuity for trees (White, 1983) and other vascular plants (Droissart et al., 2018; Marshall et al., 2021) dividing two subregions in central Africa, i.e. the Lower Guinea and Congolia subcenters of endemism though the separation between the two is much larger and corresponds to the Sangha River Interval, a 400km wide forest area (14–18°E), recognized for its low plant endemism (White, 1983). Rivers, especially large rivers (>1 km) that are not easily crossed, act as natural dispersal barriers to numerous taxa across the globe (Aliaga-Samanez et al., 2020; Chapman et al., 1999; Kingdon et al., 2013; Oliveira et al., 2017). The riverine barrier mechanism has been proposed as a possible scenario for explaining the diversification of tropical African biodiversity (Couvreur et al., 2021). In central Africa, the current river network was earlier linked to the distribution of forest primates (Colyn et al., 1991; Colyn & Deleporte, 2004), but our study formally tested the role of rivers on the whole of primate and artiodactyl assemblages. Major rivers also explained current patterns of genetic diversity among some rodent (Nicolas et al., 2011), primate (Anthony et al., 2007; Eriksson et al., 2004; Gonder & Disotell, 2006; Telfer et al., 2003) and artiodactyl (Moodley & Bruford, 2007) species. The Ogooué and Sangha Rivers, although

important drivers of genetic variation among gorilla and mandrill populations (Anthony et al., 2007; Telfer et al., 2003), were not found as major barriers differentiating primate communities at this regional scale. Also, we did not identify the Cameroon Volcanic Line as a major discontinuity for primates and artiodactyls, though it plays an important role in amphibian distributions (Portik et al., 2017). Insularity and precipitation-related variables were found to be important predictors of primate districts' distribution. Some primate species on Bioko Island are endemic like *Ptilocolobus pennantii* and differ from their sister species on the continent (Mittermeier et al., 2013) while the role of precipitation is certainly associated with changes in forest composition and functioning. Indeed, the shift between the 'Atlantic' and 'Inland' districts for primates, which closely matches the limit between the Congolian coastal forests and the Northwest Congolian lowland forests ecoregions (sensu Dinerstein et al., 2017, Appendix S3, Figure S3.1), corresponds to a shift from the wetter and less seasonal evergreen forests to the drier and more seasonal semi-deciduous forests (Fayolle et al., 2014; Réjou-Méchain et al., 2021). This shift most likely translates into differences in quality, quantity and seasonality of fruits, seeds and leaves, the main components of primate diets (Chapman, 1995; Gautier-Hion et al., 1999). For example, *Colobus satanas* is an 'Atlantic' species whose diet is primarily based on seeds (up to 60%), and evergreen forests within its distribution are extremely rich in legumes that produce many pods and seeds (Mittermeier et al., 2013). By contrast, *Colobus*

guereza is an 'Inland' species, which exhibits a flexible diet between folivory and frugivory (focusing on leaves and unripe fruit, often pods), and semi-deciduous forests stretching deeper inland are known for the greater and longer abundance of fruit (Gautier-Hion et al., 1999; Poulsen et al., 2002). This association with the forest type seems to be restricted to primates as we did not encounter a similar pattern for artiodactyls, perhaps due to their less restrictive diet than small arboreal primates. In the same line, the zoogeographical patterns obtained from the IUCN-based analysis for primates, which were highly congruent with our districts obtained from ground surveys, also provided the most refined biogeographic patterns (Appendix S2, Figure S2.1), supporting the relevance of these highly forest-dependent taxa for understanding the zoogeography of central African forests (Colyn et al., 1991; Colyn & Deleporte, 2004).

The classification of central African forest mammal assemblages we provided is also congruent with the WWF ecoregions (Dinerstein et al., 2017) that have been widely used for conservation planning (Appendix S3, Table S3.1). Here, we also detailed the conservation implications of the congruent biogeographic patterns retrieved among primates and artiodactyls from ground surveys, notably integrating protected area coverage, and levels of anthropogenic threats. Protected areas currently cover 14.2% of central African forests including all the districts we delimited. With only 12% and 11% of protected area coverage, the 'Congo-Kasaï' and 'East Congo' districts in the DRC were below the 17% threshold of protected land and inland waters advocated by the 2020 Aichi Target 11 (UN CBD, 2010). High protected area coverage, such as in the 'Rift' district (>60% for artiodactyls), should not be interpreted alone as sufficient for achieving conservation outcomes, as these areas may be heavily deforested and fragmented. By joining maps of hunting-induced defaunation (Benítez-López et al., 2019) and forest integrity (Grantham et al., 2020), we detected scattered hotspots of anthropogenic threats and very few undisturbed areas across central African forests. Indeed, almost no area in the world can be classified as faunally pristine (Allan et al., 2019; Plumptre et al., 2021), even in the tropics and within protected areas (Laurance et al., 2012). Across central African forests, 'South Nigeria' is the most strongly threatened district, with severely depleted wildlife and little forest integrity, probably due to the rise and expansion of many cities and urban centres along the coast. The high level of defaunation in the 'Cameroonian Highlands' and 'Bioko' districts is due to high human density in the Cross-Sanaga region and in Bioko, particularly around Malabo, north of the island (Fa et al., 2014). Regarding the 'Inland' district ('Inland' and 'Atlantic' for primates), the largest district according to our model's predictions, large forest tracts remain relatively undisturbed in Gabon and in the Republic of Congo, in protected areas and in their surroundings, which are mostly composed of logging concessions. This is not the case for southwest Cameroon and the southern Mayumbe forest along the coast of Congo and of the DRC, which are highly impacted by anthropogenic threats. Strong human pressure also occurs in eastern central Africa and

emerging deforestation hotspots were recently detected across most of the 'Congo-Kasaï' district and at the edge of the 'East Congo' district (Harris et al., 2017; Vancutsem et al., 2021). While vastly protected, either in the DRC (e.g. Virunga NP, Kahuzi-Biega NP) or in Uganda (e.g. Kibale NP or Bwindi Impenetrable NP), high level of threats also occurs along the Albertine Rift and its foothills making the 'Rift' district particularly at risk.

Since anthropogenic disturbances and environmental changes rapidly occur throughout central Africa (Abernethy et al., 2016) already inducing cascading effects on the megafauna (Bush et al., 2020), there is an urgent need to implement actions to conserve all identified districts. Our results call for two types of conservation policies that can be formulated in complementary ways. On one side, priority must be given to the most coveted areas already subject to strong threats, which harbour unique and highly threatened mammal assemblages such as those in the 'South Nigeria', 'Cameroonian Highlands', 'Bioko' and 'Rift' districts. In this case, the conservation of small areas through sanctuaries and community management areas must be privileged, while maintaining and connecting the existing protected areas. In these highly threatened districts, the reported species pool (Appendix S1, Table S1.1) constitutes a valuable tool for assessing potential missing species (by comparing the expected composition with the observed one) and will provide guidance for rewilding programs. On the other side, districts that are characterized by vast remote forest areas with little deforestation and low population density and already covered by several protected areas (e.g. Dzangha-Sangha NP in the 'Inland' district, the Salonga NP and Lomami NP in the 'Congo-Kasaï' district, the Hunting Domain of Rubi-Tele, Okapi Wildlife Reserve and Maiko NP in the 'East Congo' district) must remain central to conservation policies at regional and national levels. Large and relatively intact areas persist in the DRC, providing opportunities to expand the protected area network if their conservation value is confirmed by exploratory field investigations. Though vastly understudied, the country harbours future discovery potential for mammalian taxa (Moura & Jetz, 2021) as confirmed by recent (re)discoveries of species (Hart et al., 2012; Maisels & Devreese, 2020). Despite gathering data as diverse as wildlife surveys and hunting bag data, it is striking that some areas remain poorly explored and largely enigmatic regarding their mammal assemblages, even though they might represent potential new districts if better documented. Those include a large part of the 'East Congo' district, as well as the vast swampy and permanently flooded forests of the Congo River depression, including the central Congo Basin peatland complex (Dargie et al., 2017). Finally, ensuring large-scale ecological connectivity must be at the core of regional- and country-level conservation strategies, by establishing new protected areas in biologically relevant places and promoting interconnectivity between existing protected areas. Public-private partnerships could be part of these strategies integrating conservation actions in well-managed logging concessions in the periphery of protected areas (e.g. TRIDOM-TNS conservation landscape in the 'Inland' district).

5 | CONCLUSIONS

In this study, we identified and mapped central African forests' mammal assemblages using an extensive and original dataset of species lists. Both primates and artiodactyls present spatially structured assemblages, while carnivores only form a unique and broad Congolian district with no clear further divisions. We also evidenced the structuring role of rivers on both primate and artiodactyl assemblages' geographic distribution and the importance of insularity and precipitation on primate species composition specifically. Our classification into zoogeographic districts provides an important benchmark for assessing the conservation status of large mammalian fauna in the region, highlighting priority districts that are threatened and poorly represented in the protected area network. The reported species pool and indicator species from each district can also be used to identify some of the missing species in newly sampled areas and can serve as indicators to determine target species for rewilding efforts. It should be noted that our compilation of existing literature also highlights broad areas that remain understudied in central Africa, including but not limited to, large parts of the DRC and the central Congo Basin peatland complex.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Species occurrence and all survey data are available on the Dryad repository (<https://doi.org/10.5061/dryad.qjq2bvqkb>).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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