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RESEARCH ARTICLE

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Zoogeographic regionalisation of terrestrial vertebrates of Mozambique

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Abstract

During the formative years of science-based biodiversity conservation and planning, Mozambique was undergoing a prolonged post-colonial liberation struggle (1964–1974) and subsequent civil war (1976–1992), resulting in a profound gap in biodiversity knowledge and conservation planning relative to other countries in the region. This study represents Mozambique's first post-war (1992 to the present) zoogeographic regionalisation at a fine scale, using 20 years of terrestrial vertebrate data comprising 54 species and 27,199 records that cover 53% of the 0.5° grid cells of the country, with 35% of cells having sufficient data for subsequent quantitative analysis. Cluster and Indicator species (IndVal) analysis were used to delimit zooregions and to identify their characteristic species, respectively, while Redundancy analysis was used to relate environmental variables to vertebrate groups. These analyses divided Mozambique into six zooregions (Niassa, Tete, Gilé, Marromeu-Gorongosa, Limpopo-Zinave-Banhine and Maputo). Our study reveals that the zooregions identified are not adequately protected by the current network of protected areas. An expanded network of protected areas is needed to ensure biodiversity conservation in Mozambique.

KEYWORDS
Mozambique, systematic conservation planning, terrestrial vertebrates, zoogeographical regionalisation

Résumé

Au cours des premières années de la conservation et de la planification de la biodiversité fondées sur la science, le Mozambique a connu une longue lutte de libération postcoloniale (1964–1974) et une guerre civile qui a suivi (1976–1992), entraînant un profond fossé dans les connaissances sur la biodiversité et la planification de la conservation par rapport à vers d'autres pays de la région. Cette étude représente la première régionalisation zoogéographique du Mozambique d'après-guerre (de 1992 à aujourd'hui) à une échelle fine, en utilisant 20 ans de données sur les vertébrés terrestres comprenant 54 espèces et 27,199 enregistrements qui couvrent 53 % des cellules de grille de 0,5° du pays, avec 35 % de cellules ayant suffisamment de données pour une analyse quantitative ultérieure. L'analyse des groupes et des espèces indicatrices (IndVal) a été utilisée pour délimiter les zoorégions et pour identifier leurs espèces caractéristiques, respectivement, tandis que l'analyse de redondance a été utilisée pour relier les variables environnementales aux groupes de vertébrés. Ces analyses ont divisé le Mozambique en six zoorégions (Niassa, Tete, Gilé, Marromeu-Gorongosa, Limpopo-Zinave-Banhine et Maputo). Notre étude révèle que les zoorégions délimitées ne sont pas suffisamment protégées par le réseau actuel d'aires protégées. Un réseau élargi d'aires protégées est nécessaire pour assurer la conservation de la biodiversité au Mozambique.

1 | INTRODUCTION

Biogeographical regionalisation categorises geographical areas in terms of their biotas, statistically clustering homogeneous regions with similar biodiversity composition using species with a strong affinity for certain habitats as bio-indicators (Baselga et al., 2007; McGeoch et al., 2002). The bio-indicator species are used to characterise their associated biogeographical regions (bioregions) (Dufrêne & Legendre, 1997; Mateo et al., 2013). These bioregions are fundamental units in the study of species distribution patterns, and facilitate systematic biodiversity monitoring and conservation planning for terrestrial (McKenzie et al., 2007), aquatic (Dagosta & de Pinna, 2017), and marine environments (Lourie & Vincent, 2004; Roberson et al., 2017). Species distribution patterns related to bioclimatic factors also help to identify important climatic considerations for plant and animal species conservation (Brito et al., 2016; Michalak et al., 2018), especially with respect to climate change (Donlan, 2013).

Previous efforts to develop biogeographical regions for Mozambique's terrestrial fauna have been limited to continental (Linder et al., 2012; Turpie & Crowe, 1994) and global scales (Ficetola et al., 2017). Linder et al. (2012) using mammalian, reptilian, avian and floral data produced a biogeographical regionalisation of Sub-Saharan Africa, which allowed the identification of two biogeographical regions in Mozambique, namely, Zambezian and Southern Africa. The Zambezian region occupies more than 80% of the territory of Mozambique, while the South African region occupies only a small portion of the Far South West of Mozambique (Linder et al., 2012). While large-scale bioregionalisation is valuable for regional planning efforts (Terauds & Lee, 2016), finer-scale bioregionalisation within Mozambique is vital for determining national-level conservation policies, strategies and protected area networks (Olivero et al., 2013).

For terrestrial wildlife, it is essential to understand the suitability of available wildlife habitat per biogeographical (zoogeographical) region to develop appropriate conservation measures (Peixoto et al., 2020). Historically, protected areas in Mozambique were established by professional hunters and wildlife enthusiasts without the use of scientific criteria to identify species requirements or maintain ecosystem functioning (Neumann, 1996). Consequently, some ecologically important areas have been placed outside the scope of the national network of protected areas of Mozambique (Fajardo et al., 2014). This has resulted in insufficient protection of several vital areas for biodiversity conservation in Mozambique, and these unprotected sites have significantly degraded over time (Gaston et al., 2008; Olivero et al., 2013). Reassessing the national wildlife conservation strategy for Mozambique using zoogeographical regionalisation therefore offers an opportunity to improve the protected area system and restore damaged areas. Zoogeographic region data also may contribute to better planning for the re-introduction of wildlife species that were locally extirpated during the prolonged period of armed conflict in Mozambique between 1975 and 1990.

This study describes the first attempt at establishing a national zoogeographic regionalisation for Mozambique. The objectives of the study were to: (1) Compile terrestrial vertebrate data for Mozambique from all reliable records, with emphasis on post-war distribution of wildlife; (2) apply these data to statistically delimit zooregions for terrestrial vertebrates; (3) identify environmental factors that may influence the distribution of terrestrial vertebrates in the delimited regions; (4) identify the vertebrate indicator species that characterise each zooregion; and (5) Assess wildlife conservation opportunities within each of the identified biogeographical regions.

2 | METHODS

2.1 | Study area

Mozambique (799,380 km^2) extends 2700 km along the Indian Ocean coast and is divided into 10 provinces and two major topographic regions (Figure 1). North of the Zambezi River in central Mozambique is a narrow coastline and bordering plateau that slopes up-wards into hills and a series of rugged highlands such as Angonia and Lichinga Highlands with scattered mountains (Toté et al., 2015). South of the Zambezi River, the lowlands are much wider with scattered hills and mountains along its borders with South Africa, Swaziland and Zambia (Toté et al., 2015; Figure 1). The climate of Mozambique is tropical with dry and wet seasons (Toté et al., 2015). Precipitation is higher along the coast than the interior, and highest in central

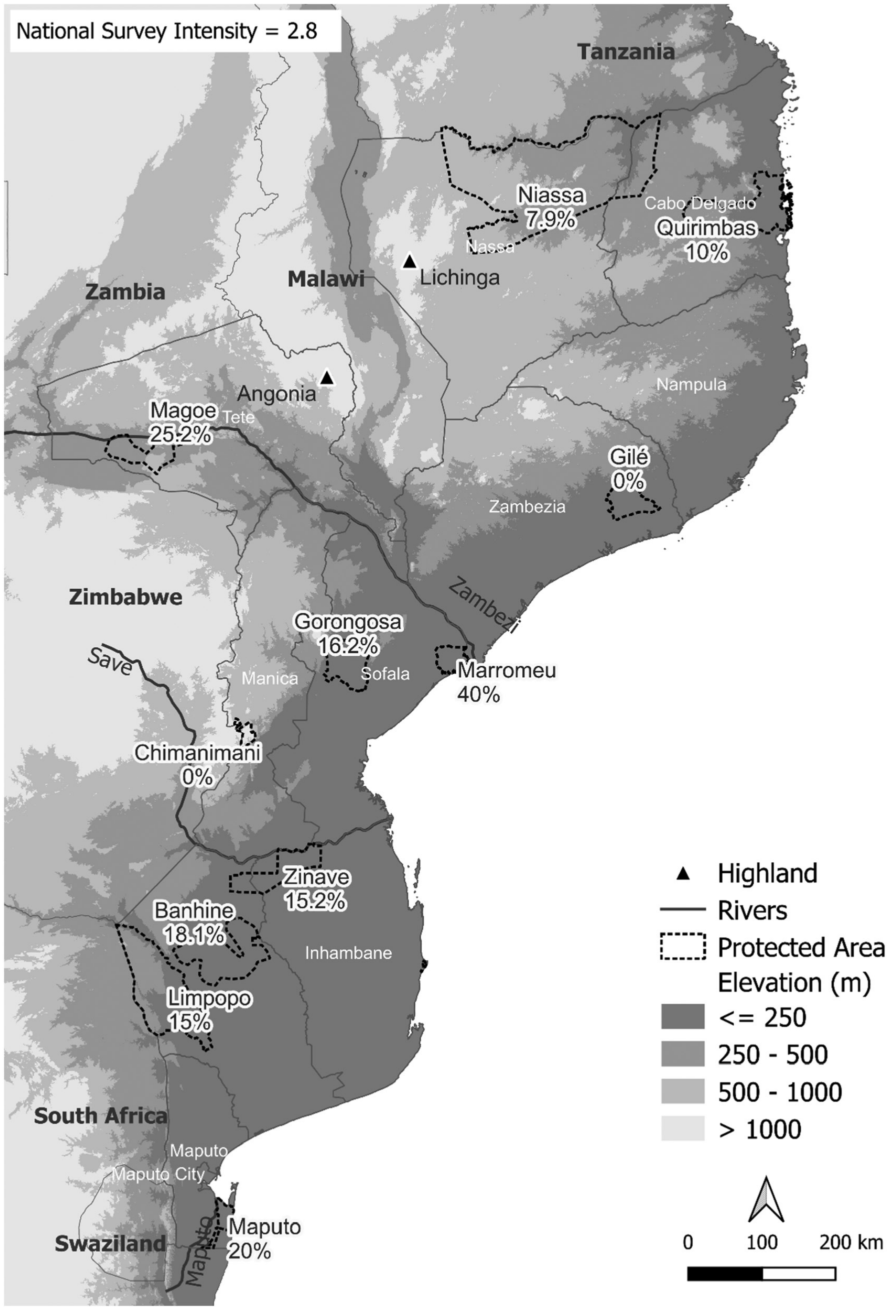

FIGURE 1 Provinces, protected areas, the main topography of Mozambique, and their associated aerial survey intensities.

Mozambique (Smithers & Tello, 1976). The average temperature increases from south to north and is higher along the coast relative to the interior (MICOA, 2007). The population of Mozambique is about 31 million people (36 people/km^2), 67% of whom live in rural areas (VRN, 2020), often in close proximity to conservation areas.

2.2 | Species data

Vertebrate data were obtained from aerial surveys conducted between 2000 and 2014 covering medium to large-sized terrestrial vertebrates that can be easily detected from the air (see Fleming & Tracey, 2008 for a discussion of factors that influence species detectability). Due to the lack of animals in Gilé National Park during aerial counts carried out in 1997 (Chande et al., 1997), we had to include ground survey data. Ground surveys aimed to cover species that are poorly detected during aerial surveys (e.g., small, inconspicuous, nocturnal, static in response to aircraft, or occur under dense canopy). Terrestrial surveys are more accurate animal estimates despite having the disadvantage of covering small areas during surveys (Jachmann, 2002). However, species not detectable from the air were excluded from biogeographical analyses. Exclusion was based on nocturnal habits and smaller size than the oribi, which some species had in the database. Aerial surveys covered protected areas including national parks and reserves and hunting concessions. To address data gaps for areas that were difficult to access by air, including protected areas with very low wildlife densities and rural areas with scattered wildlife populations outside protected landscapes, we supplemented these surveys with data from the national aerial census of terrestrial vertebrates (Agreco, 2008). The surveys followed standardised procedures used for most aerial surveys in the region. The country was subdivided into flat and mountainous areas. On flat surfaces, surveys were undertaken based on transects and in mountainous areas with the block sampling system, for safety reasons. It consisted of demarcating an area into small sampling units using physical characteristics present in the terrain. Sampling units were randomly selected and total counts were performed for an indefinite period. The transects were systematic with a north–south orientation. The spacing between transect lines was 15 km long, 400 m in width.

During the surveys, the aircraft flew at a speed of approximately 200 km h^{-1} and an average height of 100 m above ground level. Large cities and large lakes were excluded from the surveys. In cases where conservation areas had been surveyed recently (within 5 years), we used those data rather than repeating a new survey. Sampling intensity varied within the conservation areas, with the Marromeu Complex presenting the highest intensity of 40% while the Niassa Reserve and the respective hunting blocks had the lowest intensity of 7.9%. The survey intensities in Maputo, Limpopo, Banhine, Zinave, Gorongosa, Quarimbas and Magoe National Parks were 20%, 18.1%, 18.1%, 18.1%, 10.5%, 10% and 25.2%, respectively. In Chimanimani and Gilé National Parks, there was only aerial reconnaissance and not proper sampling. The only national survey that excluded the sampled conservation areas had a sampling intensity of 2.8% (Figure 1). A total of 27,199 records covering 54 species were obtained from all surveys (Data S1), where the taxonomy was based on Skinner and Chimimba (2005) for mammals, Sinclair and Ryan (2010) for birds and Branch (1998) for reptiles.

2.3 | Bioclimatic variables

Data were obtained from WorldClim (https://www.worldclim.org/data/worldclim21.html) accessed on 01 June 2020) (Hijmans et al., 2005). The data selected included 19 monthly temperature and precipitation variables (Table 1) recorded between 1950 and 2000. Altitude data were obtained from the Shuttle Radar Topography Mission (SRTM; https://gisgeography.com/srtm-shuttle-radar-topography-mission/ accessed on 01 June 2020) radar data, version 4.1 (Jarvis et al., 2008). To deal with collinearity and improve the interpretability of our analysis, we followed a two-step approach. We first identified clusters for all 20 variables using the function "removecollinearity" from the "virtualspecies" R package (Cotrina-Sánchez et al., 2021; Leroy et al., 2016). The variables were clustered according to a Pearson correlation coefficient of $r = 0.65$. We retained for subsequent analysis the

TABLE 1 Bioclimatic variables used for delimiting zooregions in Mozambique. Bold represents retained and uncorrelated variables used in subsequent analyses.

	Bioclimatic variable	Measurement units
1	BIO_1: Annual mean temperature	°C
2	BIO_2: Mean diurnal range [Mean of monthly (max temp − min temp)]	°C
3	BIO_3: Isothermality	%
4	BIO_4: Temperature seasonality (standard deviation × 100)	%
5	BIO_5: Max temperature of warmest month	°C
6	BIO_6: Min temperature of coldest month	°C
7	**BIO 7: Temperature annual range (BIO5–BIO6)**	°C
8	BIO_8: Mean temperature of wettest quarter	°C
9	**BIO_9: Mean temperature of driest quarter**	**°C**
10	BIO_10: Mean temperature of warmest quarter	°C
11	BIO_11: Mean temperature of coldest quarter	°C
12	**BIO_12: Annual precipitation (mm $year^{-1}$)**	**mm $year^{-1}$**
13	BIO_13: Precipitation of wettest month	mm $month^{-1}$
14	BIO_14: Precipitation of driest month	mm $month^{-1}$
15	BIO_15: Precipitation seasonality (coefficient of variation)	%
16	BIO_16: Precipitation of wettest quarter	mm $month^{-1}$
17	BIO_17: Precipitation of driest quarter	mm $month^{-1}$
18	**BIO_18: Precipitation of warmest quarter**	**mm $month^{-1}$**
19	BIO_19: Precipitation of coldest quarter	mm $month^{-1}$
20	**Alt: Altitude**	**meter**

single variables selected randomly by the "removecollinearity" function from each cluster. Our second step was to use Principal Component Analysis (PCA), which represents a common technique used to deal with collinearity among variables by creating new, uncorrelated orthogonal axes (Dormann et al., 2013). The original raster files of the subset of variables with 250 m pixel size were superimposed onto 0.5° grid cells covering the Mozambican national territory to obtain mean values at each grid cell. For altitude, we used the modal value at each 0.5° grid cell. We investigated and retained the original variables that contributed most to the explained variance in the first and second principal components by using the "fviz_contrib" function in the FactorExtra package (Le et al., 2008), instead of using new orthogonal axes. Five uncorrelated variables with the highest explanatory power were used for subsequent analysis (variables marked in bold in Table 1; Appendix S1).

2.4 | The identification of biogeographic regions

To minimise the impact of spatial sample bias, 0.5° grid squares (~55 km^2) were selected to aggregate distributional data (He et al., 2017; Rodrigues et al., 2015). Multivariate analyses were used to delimit faunal regions quantitatively (Kreft & Jetz, 2010) for the stratification of 0.5° grid cells. Mozambique comprises 347 0.5° grid squares, 183 of which (53%) had vertebrate data. Our study was affected by the concentration of sampling effort in national parks and reserves (Figure 1), as these sites were a post-civil war government priority to reactivate wildlife conservation activities, which had been halted. This gap can contribute to the erroneous identification of biogeographical regions with little data (Rodrigues et al., 2015). To reduce bias resulting from insufficient or uneven sampling (Yusefi et al., 2019), all grid squares with less than three species were excluded from subsequent analyses (Kreft & Jetz, 2010), resulting in 123 grid squares being analysed for the zoogeographic regionalisation of terrestrial vertebrate species (35%) (Figure 2).

Cluster analysis was used to spatially group terrestrial vertebrate species using a fuzzy pair-wise similarity matrix between pairs of grid cells with the "fuzsim function" in "fuzzySim" package (Barbosa, 2015), as it ensures zoogeographical regions are more likely to be robust to disparities, errors or gaps in species occurrence data, even for narrowly distributed species (Barbosa, 2015). We used dissimilarities as 1 − fuzzy similarity. We built dendrograms for two similarity indices Jaccard (1901) and Baroni-Urbani and Buser (1976) in "fuzzySim" package (Barbosa, 2015), and two clustering methods (Ward's and Average) in "hclust function" in the Stats R package (R Core Team, 2021). We retained the dendrogram resulting from Jaccard distance and the linear unweighted pair group method with arithmetic mean (UPGMA) agglomerative method as it scored the highest correlation between the dissimilarity matrix with the co-phenetic distance using the "cophenetic" function in Stats R package (Kreft & Jetz, 2010).

A variety of methods are used to define the appropriate number of groups in cluster analysis (Kreft & Jetz, 2010; Milligan & Cooper, 1985). To establish a coherent number of groups of faunal regions, we followed a compromise between: (1) inspecting the height of nodes in the dendrogram, considering that high levels in the dendrogram are less informative (Kreft & Jetz, 2010); (2) observing all validation measures for clustering in "clValid" package (Brock et al., 2008) by building the analysis for "internal" (Connectivity, Silhouette Width, and Dunn) and "stability" (APN, AD, ADM and FOM) metrics using average distances and hierarchical clustering over the same original dissimilarity matrix; and (3) evaluating the spatial distribution of the groups by mapping to verify spatial coherence, and choosing the number of groups maximising spatial interpretation. The optimal cluster number resulting from "clValid" retains the first index (i.e., number of clusters) that maximises the metric. We visually checked "clValid" plots, to find which cluster number matches the best solution at each metric and the ranked order of each cluster number evaluated from the distance to the optimal solution proposed by the "clValid" function.

In the analysis of zoogeographical regionalisation, medium and large-sized terrestrial vertebrate species were involved, corresponding to 44 of the 54 species in the database (Appendix S2 and Data S1). The purpose was to determine the type of species most relevant in defining zoogeographical regions in Mozambique. Following Fernández and Vrba (2005), medium-sized terrestrial vertebrate species were defined as having a body mass ranging from 5 to 100 kg, while large-sized vertebrate species were defined as those weighing >100 kg. For a visual interpretation of regions associated with the terrestrial vertebrates, clusters of grid cells were converted into a net of polygons of Thiessen to provide a simplified visualisation (Rodrigues et al., 2015).

2.5 | Indicator species

The Indicator Value (IndVal; Dufrêne & Legendre, 1997) was computed for each terrestrial vertebrate species after defining the appropriate number of clusters. IndVal value (on a scale of 0–1) represents the degree of specificity and fidelity of each species to a biogeographical region (McGeoch et al., 2002). A species was considered an indicator species for a specific bioregion if its IndVal was >0.50 and $p \le 0.05$. Species for whose IndVal is ≤0.5 are considered generalist, but we must emphasise that by taking presence/absence data only, IndVal fidelity will represent a measure of concentration (Podani & Csányi, 2010). To overcome this constraint, we investigated indicator species with the multi-level pattern analysis using the "multipatt" function in the "indicspecies" package (De Cáceres & Legendre, 2009) using the original IndVal association index by selecting the "IndVal.g" option. Statistical significance was evaluated from 999 re-sampling permutations. No emphasis is given in the discussion to nocturnal indicator species obtained from the ground survey.

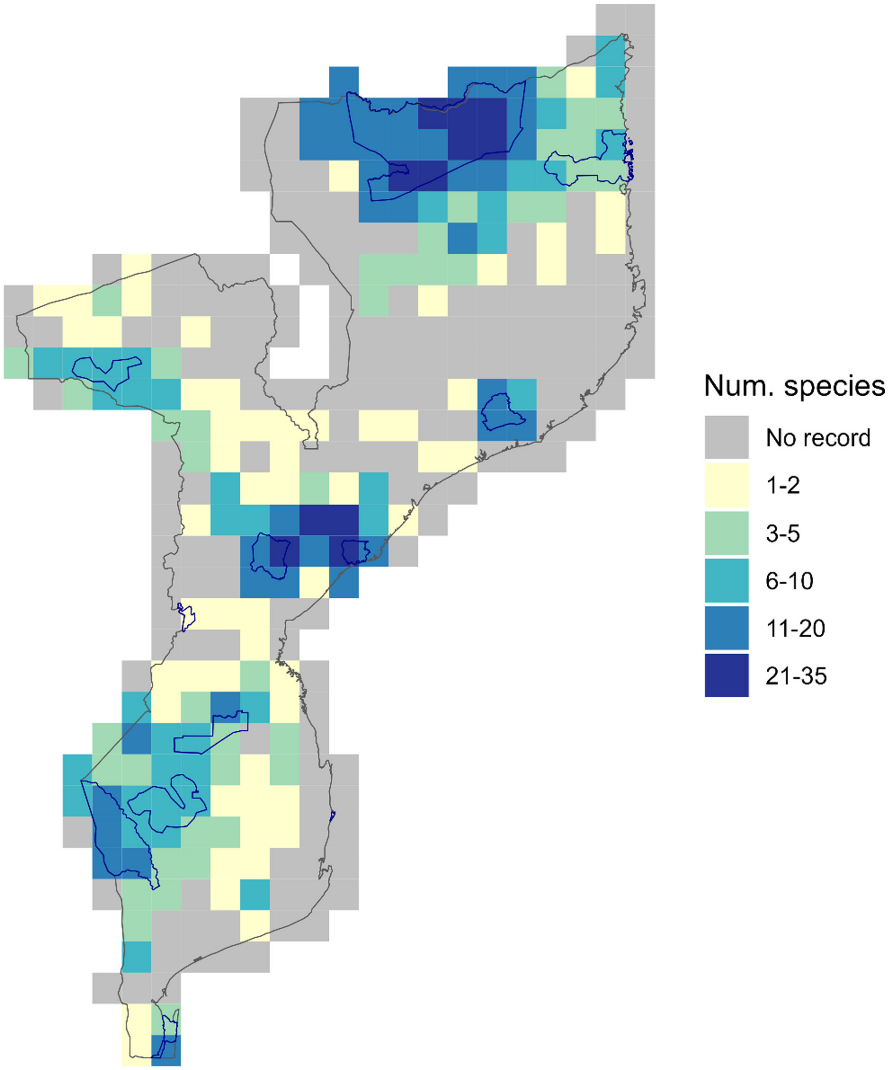

FIGURE 2 Species richness and number of species per 0.5° grid cells obtained from aerial surveys in Mozambique between 2000 and 2014. Grid cells with less than three species were excluded from analysis. Species were recorded from 183 cells representing 53% of the total area of Mozambique. Blue polygons represent terrestrial protected areas in Mozambique.

2.6 | The relationship between environmental variables and terrestrial vertebrate groupings

Distance-based redundancy analysis (db-RDA; Legendre & Anderson, 1999) was used to assess the association between bioclimatic variables and vertebrate groupings and to provide an ecogeographic interpretation of identified biogeographic regions. We used analysis of variance (ANOVA) to test the statistical significance of the general ordination analysis, the axes, and the five bioclimatic variables retained for this analysis. For the interpretation of ecogeographical patterns, we built triplots from db-RDA with the ellipses of the biogeographic regions (clusters) superimposed.

2.7 | Wildlife conservation opportunities

We assessed the adequacy of the protected area network (PA) as the gap between protected area coverage at each region and the unrealised area available for protection at each bioregion. We estimated the unrealised area available for protection as the territory not covered by human settlements (i.e., urban, communal areas) and agriculture. Land cover was obtained from Hatton et al. (2001) (agricultural areas presented in Appendix S3). Protected Areas from Categories I to VI under the International Union for Conservation of Nature (IUCN) Protected Area Category System (Dudley, 2008) and strictly or partially managed by the government were used for PA coverage evaluation (Table 2), with polygons obtained from World Data Base on Protected Areas (WDPA; https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA accessed on 13 June 2020). In Mozambique, this included national parks, national nature reserves, and a few hunting concessions. All analyses in the present study were undertaken using algorithms in R (R Core Team, 2021).

3 | RESULTS

3.1 | Species

Six groups were analysed (Table 3, and a species summary is indicated in Appendix S2). During the counts, there were 27,066 records of occurrences of terrestrial vertebrates. The total percentage of

TABLE 2 Terrestrial protected areas in Mozambique and their categorisation according to the International Union for Conservation of Nature (IUCN) criteria.

Protected area	Province	Area (km^2)	IUCN category
Banhine National Park	Gaza	7250	II
Chimanimani National Park	Manica	6550	II
Gorongosa National Park	Sofala	5370	II
Limpopo National Park	Gaza	11,233	II
Magoe National Park	Tete	3558	II
Quirimbas National Park	Cabo Delgado	9130	V
Zinave National Park	Inhambane	4000	II
Gilé National Reserve	Zambezia	4436	II
Maputo Special Reserve	Maputo	1040	IV
Marromeu National Reserve	Sofala	1500	IV
Niassa National Reserve	Niassa	42,200	VI
Pomene National Reserve	Inhambane	50	IV

Note: Only IUCN categories I–VI, strictly or co-managed by the government and covering terrestrial habitats were used for analysis. Polygons were obtained from World Data Base on Protected Areas (WDPA; https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA accessed on 13 June 2020).

TABLE 3 A summary of taxonomic groups and their occurrence in Mozambique considered for zooregion analysis.

Taxonomic group	Number of occurrences	Number of species	Number of grid cells
Ungulates	23,090	25	167
Aves	1170	8	100
Carnivores	46	6	24
Primates	482	3	76
Megaherbivores	2048	1	92
Reptiles	230	1	38
Total	27,066	44	497

the 10 most observed species was 80% and are distributed as: (1) common duiker (*Sylvicapra grimmia*) – 21.15%; (2) common warthog (*Phacochoerus africanus*) – 9.80%; (3) sable (*Hippotragus niger*) – 8.34%; (4) southern reedbuck (*Redunca arundinum*) – 7.56%; (5) African savanna elephant (*Loxodonta africana*) – 5.37%; (6) oribi (*Ourebia ourebi*) – 3.13%; (7) southern ground hornbill (*Bucorvus leadbeateri*) – 3.13%; (8) greater kudu (*Tragelaphus strepsiceros*) – 2.99%; (9) waterbuck (*Kobus ellipsiprymnus*) – 2.97%, and (10) bushbuck (*Tragelaphus scriptus*) – 2.97% (Table 3; Appendix S2). These species were frequently observed in their places of occurrence during aerial surveys. The most widely distributed species across Mozambique occurring in most areas surveyed included: (1) African buffalo; (2) common warthog; (3) common duiker; (4) southern reedbuck; (5) African savanna elephant; (6) greater kudu; (7) impala (*Aphyceros melampus*); (8) blue wildebeest; (9) waterbuck; (10) Sharpe's grysbok (*Raphicerus sharpei*); and (11) bushpig (*Potamochoerus larvatu*). These species occur throughout the country (i.e., in most of the 183 grid cells with available data) (see details in Data S1).

3.2 | Zoogeographic regions and indicator species

The analysis of medium and large sized vertebrates species suggested dividing Mozambique into six zooregions ($K=6$) namely, (1) Gilé (G); (2) Limpopo-Zinave-Banhine (LZB); (3) Maputo (M); (4) Marromeu-Gorongosa (MG); (5) Niassa (N), and (6) Tete (T) (Figure 3). The validation measures for clusters in the "clValid" package suggested two cluster modal values, $K=5$ and $K=7$. We therefore used the intermediate modal value of the cluster (i.e., $K=6$) as the ideal value (Appendix S4). The ideal cluster value was complemented by superimposing two dendrograms generated by different methods, as the interlaced lines were minimal with $K=6$. The first cluster separated three well-defined regions distributed between the North, Central and South zones ($K=3$) of Mozambique. The second cluster kept the North and Central zones and cut the South zone, generating the Maputo region ($K=4$). The third cluster simultaneously separated the North and Central zones, creating the Gilé and Tete zones (Appendix S5). The high cophenetic correlation coefficient (cor = 0.88) strongly validates the results obtained. It was possible to calculate statistically significant Indicator values (IndVal) for 26 species, with each species demonstrating to be associated with at least one zooregion identified as follows: (1) Niassa with two species; (2) Marromeu-Gorongosa with six species; (3) Maputo with four species; (4) Gilé with 12 species; and (5) Limpopo-Zinave-Banhine and (6) Tete with 1 species each. Only two species qualified as indicator species for their respective zooregions, as their IndVal values were ≥0.5. In this regard, the Maputo zooregion is associated with the presence of the plains zebra (*Equus quagga*) (IndVal = 0.50; $p < 0.5$), while the Gilé zooregion is associated with the red antelope (*Cephalophus natalensis*) (IndVal = 0.55; $p < 0.5$). The other zooregions revealed the presence of generalist species whose association was not strictly linked to those particular zones.

3.3 | Environmental correlates of zoogeographic regionalisation

Person's correlation analysis identified five least correlated environmental variables (i.e., $r < 0.65$) among the 20 variables analysed (Table 1). The five variables were subsequently used in the redundancy analysis (dbRDA; Appendix S1), and these included: (1) altitude (mod_alt); (2) annual temperature range (bio_7); (3) mean driest quarter (bio_9); (4) annual precipitation (bio_12) and (5) warmest quarter precipitation (bio_18). The dbRDA showed that the first two canonical axes (CAP1 and CAP2) explained 86.07% of the total variance and were statistically significant (Figure 4). CAP1 ($F = 67.88$; $p = 0.001$) explained 63.33% of the total variance in 46% of the studied species and was positively correlated with altitude (mod_alt), average temperature of the driest quarter (bio_9), annual precipitation (bio_12) and annual temperature variation (bio_7); and negatively correlated with annual temperature range (bio_7). CAP2 ($F = 25.31$; $p = 0.001$) explained 22.74% of the total variance of 52% of the studied species and was positively correlated with precipitation in the warmest quarter (bio_18) (Figure 4).

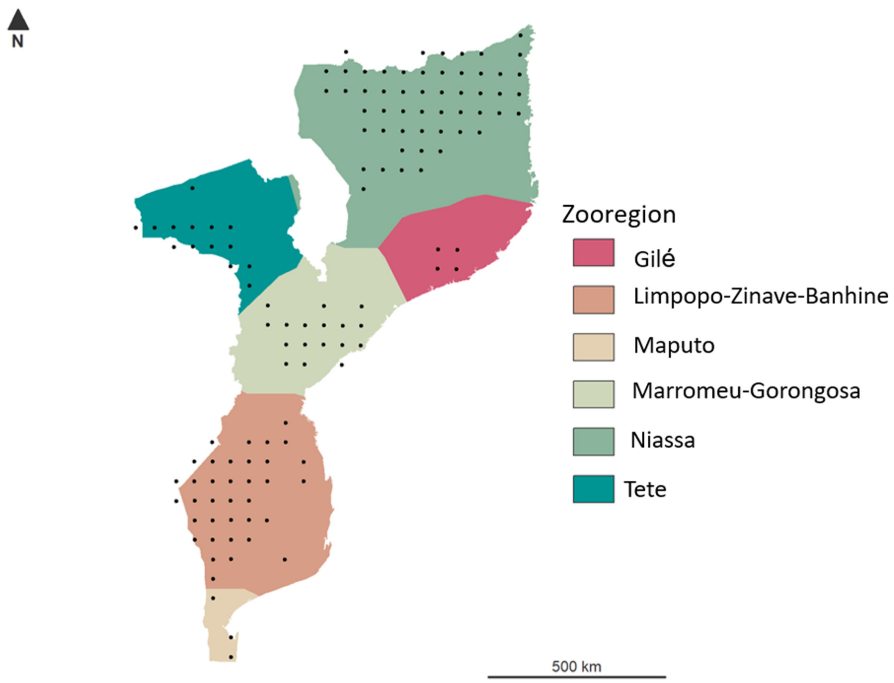

FIGURE 3 A map of Mozambique showing its six delimited zooregions based on a cut-off of a cophenetic correlation coefficient of 0.88 using medium- and large-sized vertebrate species surveyed between 2000 and 2014. G, Gilé; LZB, Limpopo-Zinave-Banhine; M, Maputo; MG, Marromeu-Gorongosa; N, Niassa; T, Tete zooregions. Black dots represent 0.5° grid cell centroids considered for delimiting zooregions in Mozambique.

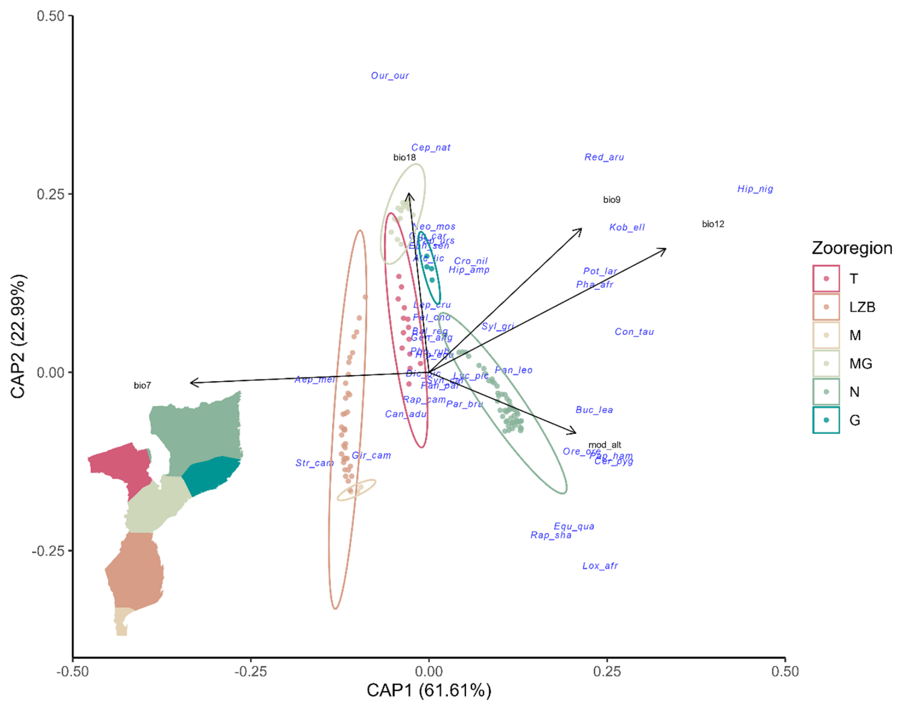

FIGURE 4 An ordination scatterplot from a distance-based redundancy analysis (db-RDA) of bioclimatic variables, sites per 0.5° grid cells, and the distribution of terrestrial vertebrate species in Mozambique. Species abbreviations are presented in Appendix S6.

Five of six identified zooregions were totally or partially associated with precipitation of the warmest quarter (bio_18), with most species being associated with its gradient. The species mostly associated with a gradient of bio_18 included: (1) suni (*Neotragus moschatus*); (2) wattled crane (*Grus carunculatus*); (3) red forest duiker (*Cephalophus natalensis*); (4) Nile crocodile (*Crocodylus niloticus*); (5) hippopotamus (*Hippopotamus amphibius*) and (6) aardvark (*Orycteropus afer*). Niassa zooregion was associated with altitude, and partially by: (1) annual thermal amplitude (bio_7); (2) mean driest quarter (bio_9) and (3) annual precipitation (bio_12). Altitude (mod_alt) and its gradient were associated with the second highest number of species that included: (1) the ground hornbill (*Bucorvus leadbeateri*); (2) klipspringer (*Oreotragus oreotragus*) and (3) vervet monkey (*Cercopithecus pygerythrus*). Other variables and their associated gradients were associated with only a few species and included: (1) annual thermal amplitude (bio_7) associated with impala (*Aepyceros melampus*) and (2) annual precipitation (bio_12) associated with warthog (*Phacochoerus africanus*) (Figure 4).

3.4 | Wildlife conservation opportunities

The Niassa zooregion covers an area of 271,641.00 km^2 followed by the Limpopo-Zinave-Banhine zooregion that covers an area of 183,902.30 km^2 (Table 3), Marromeu-Gorongosa, Tete and Gilé zooregions cover an area of 132,058.90, 105,902.30 and 76,606.40 km^2, respectively, Maputo zooregion the covers the smallest area of 18,120.60 km^2 (Table 3). The Limpopo-Zinave Banhine zooregion has five areas proclaimed for the conservation of terrestrial vertebrates, followed by the Marromeu-Gorongosa zooregion with three and Niassa zooregion with two, while the Tete, Gilé and Maputo zooregions have one area each proclaimed for conservation. The Niassa zooregion has the largest protected extension area (16% of its area) for conservation, followed by Limpopo-Banhine-Zinave (12.2%), Maputo (5.7%), Marromeu-Gorongosa (4.4%), Gilé (3.73%) and Tete (3.2%) zooregions (Table 3).

4 | DISCUSSION

The terrestrial vertebrate data sampled in the post-civil war period identified six zooregions in Mozambique. Each of the zooregions is configured based on the gradient variation of the environmental variables to which each species is associated. Each identified zooregion is represented in the national network of protected areas. However, most zooregions do not have a good representation, with the need to expand or develop new areas for biodiversity conservation, especially in the less extensive zooregions.

Aerial censuses directed at some national parks, nature reserves and hunting concessions, whose restoration was a priority during the post-civil war period in Mozambique, resulted in the compilation of data for 27,066 individuals representing 44 species (Appendix S2). The discrepancy in the sampling effort was foreseen, as it depended on budgetary constraints and the interest of investors and donors in restoring tourism activities and biodiversity conservation in some areas considered charismatic (Hatton et al., 2001). These limitations may have affected the distribution of available data on the species under study and consequently may have influenced the identification of zooregions. However, data from the wildlife national aerial census (Agreco, 2008) certainly minimised this limitation, as it prioritised counts outside the protected areas, in almost the entire country. Additionally, the identified zooregions have a close connection with environmental factors, which may validate the results in the present study. There is an overlap of the six identified zooregions ($K=6$) with the six main plant communities, which include the centres of endemism in Mozambique (Hatton et al., 2001). The overlap is not extensive due to the presence of cross-cutting species in the different plant communities, but it shows consistency in the results. On the contrary, replacing the sampling effort with the number of vertebrate records per grid cell did not affect the dbRDA results (Barbosa et al., 2010). This suggests a minimal effect of the sample bias on the observed patterns, therefore, placing some degree of confidence in the results obtained in the study. A similar study undertaken in Angola reached similar conclusions as in our study (Rodrigues et al., 2015). We therefore, suggest the delimitation of Mozambique into six zooregions that include: (1) Gilé (G); (2) Limpopo-Zinave-Banhine (LZB); (3) Maputo (M); (4) Marromeu-Gorongosa (MG); (5) Niassa (N) and (6) Tete (T) (Figure 3). Most of the identified zooregions represent sub-divisions of the previously recognised Zambezian region, except for the extreme south of Mozambique which falls within the South African region (Linder et al., 2012).

The subdivision of Mozambique into three regions (i.e., North, Central and South regions) ($K=3$; Appendix S5) reflects the Phyto-Edaphic zones proposed by Tinley (1977) namely: (1) the combination of Moist Savanna/Mesic forest (annual precipitation >1000 mm) with Mesic Savanna/Dry Forest (annual precipitation 600–1000 mm) in the North region; (2) the predominance of the Moist Savanna/Mesic Forest with portions of the Rain Forest (annual precipitation >2000) in the highlands in the Central region and (3) the predominance of the Arid Savanna (annual precipitation <600) in the west of the South Region. The separation of the South Zone into two parts in which the southern end is evident ($K=4$; Appendix S5) may not be surprising, as it highlights units of the greater Maputaland-Pondoland-Albany region of endemism. The subdivision highlights the regions of Southern Maputaland (Perera et al., 2011) identified as Maputo zooregion and Mozambique Lowveld identified as Limpopo-Zinave-Banhine-zooregion, which stands out using both plants and vertebrates (Perera et al., 2011). Our data had the limitation of detecting the finer-scale subdivisions of this centre of endemism, due to the dominance of medium and large-sized mammals species in the data. The data involved in the biogeographic delimitation of this centre of endemism included smaller vertebrates species (Perera et al., 2011). The distinction of the Maputaland centre of endemism may provide confidence in the definition of zooregions in our study, since the precise delimitation of this area may represent real differences in species composition and the difference in the influence of bioclimatic variables. The approach to validating biogeographic regions using the congruence of different methods (i.e., Baroni Distance vs. Linear UPGMA agglomerative methods) has been applied by several previous studies (He et al., 2017; Rodrigues et al., 2015; Yusefi et al., 2019). The Maputo zooregion does not have a clear association with selected environmental gradients. The Limpopo–Zinave Banhine zooregion extends from the north of the Incomati River to the Save River. This zooregion has a partial positive response to precipitation from the warmer quarter gradient, while the extreme west is more related to dry conditions.

The subdivision of the central zone into Marromeu-Gorongosa and Tete zooregions ($K=5$) reflects the dry gradient increasing from the coast to the west. The difference can be observed from the vegetation combination in which the west is dominated by mopani and the east by Miombo (Hatton et al., 2001; Tinley, 1977). The Marromeu-Gorongosa zooregion responds entirely and positively to the precipitation of driest quarter gradient, while the Tete zooregion responds partially (Figure 4). This variable represents the total precipitation during the 3 hottest months of the year, useful for examining factors that may affect the seasonal distribution of species (O'Donnell & Ignizio, 2012). Surprisingly, the northern zone was separated into Gilé and Niassa zooregions. This subdivision is explained by the fact that Gilé zooregion responds positively to two environmental variables namely altitude and precipitation from the warmer quarter and their associated gradients. The geographic location of Gilé and the associated environmental factors suggest that this zooregion has some environmental features of the Marromeu-Gorongosa zooregion and also features of the Niassa zooregion (Figure 4). The Niassa zooregion is positively associated with an altitudinal gradient, and partially by average annual precipitation. The Marromeu-Gorongosa zooregion is associated with the red duiker (*Cephalophus natalensis*), while the Niassa zooregion is associated with the plains zebra (*Equus quagga quagga*) as an indicator species. The same species were identified when using a different method to validate them as indicator species (Appendix S6). The remaining species do not qualify as indicator species as they were also found in different identified zooregions.

Comparing the precipitation of the warmest quarter with topography suggests that in Mozambique, precipitation of the warmest quarter is influenced by orographic rains, where the moisture coming from the Indian Ocean encounters a barrier that forces it to rise, creating precipitation mainly on the east face (Tinley, 1977). A significant percentage of the species investigated in this study are associated with the precipitation of the warmest quarter. The associated gradient of precipitation of the warmest quarter is well-represented in the Marromeu-Gorongosa zooregion, which harbours the majority of the wildlife population in Mozambique. However, on a small scale, this gradient is represented along the coast of Gilé and Niassa zooregions, and marginally in the extreme west of the Limpopo-Zinave zooregion along the chain of the Libombo Mountains. Precipitation of the warmest quarter and annual precipitation gradients were used and found to be relevant in a zoogeographic regionalisation exercise of Angola based on vertebrate species (Rodrigues et al., 2015). Given the localised precipitation of the warmest quarter and its importance in the distribution of wildlife, it could be useful in the delineation of some hotspots for the conservation of biodiversity in Mozambique. The remaining species showed a low-to-moderate association with the bioclimatic variables that were used in the present study. A similar approach for the identification of important areas for the conservation of biodiversity in Iran has previously been proposed by Yusefi et al. (2019).

Our study revealed that each zooregion identified in Mozambique is represented by at least one protected area. However, most of the identified zooregions identified in the country are not adequately represented in the current national network of protected areas. This is most prominent in the Maputo, Tete, Marromeu-Gorongosa and Gilé zooregions (Table 4). The Niassa and Limpopo-Zinave-Banhine zooregions however, are the only delineated zooregions whose protected area has managed to reach the 10% target stipulated by the IUCN to protect ecological regions (IUCN ESARO, 2020). The Maputo zooregion is of special concern due to its small size and its location in the greater Maputaland-Pondoland-Albany region of endemism. The area harbours several endemic vertebrate and plant species that are in critical need of attention for their protection (Perera et al., 2011).

This present study's first attempt to delineate zooregions in Mozambique based on terrestrial vertebrate species, and all its identified zooregions in the process, with the exception of the Gilé zooregion, have the potential for cross-border cooperation in the conservation of biodiversity. A transboundary approach to the conservation of biodiversity is cost-effective and allows for the protection of large areas. The Limpopo-Banhine-Zinave zooregion can serve as an ideal example of the advantages of this type of cooperation, as it extends to the Kruger National Park (KNP) in South Africa and Gonarezhou National Park in Zimbabwe. This transboundary conservation region covers approximately 35,000 km^2, with a potential of expanding to approximately 100,000 km^2, and would facilitate the protection of natural ecosystems as well as their functionality, making it a successful conservation area despite other potential constraints (Ntuli et al., 2021). The transboundary approach can be extended to the other zooregions in Mozambique, as the potential for extension exists for all identified zooregions in the present study. Studies undertaken in China reported on the benefits of cross-border cooperation in the conservation of biodiversity (Wu et al., 2011). On the other hand, new areas can also be proclaimed to improve the conservation representativeness of poorly protected zoom regions.

5 | CONCLUSIONS

Based on the distribution of terrestrial vertebrates in Mozambique, the following six zooregions were identified in this study: (1) Gilé (G); (2) Limpopo-Zinave-Banhine (LZB); (3) Maputo (M); (4) Marromeu-Gorongosa (MG); (5) Niassa (N) and (6) Tete (T). The critical bioclimatic variables in delimiting these zooregions in Mozambique are

TABLE 4 Wildlife conservation opportunities in delimited zooregions in Mozambique based on terrestrial vertebrate species.

Zooregion	Total area (km^2)	% of territory	Unsuitable area for conservation (km^2)	Protected by conservation area (km^2)	Available area for conservation (km^2)	% Available area for conservation (%)	Protected area (PA)
Tete	105,812.4	0.13	6380.8	3558.7	95,872.9	90.6	Magoé
Limpopo-Banhine-Zinave	183,902.3	0.23	20,407.4	22,456.5	141,038.4	76.7	Limpopo, Banhine, Zinave & Pomene
Maputo	18,120.6	0.02	1064.2	1035.9	16,020.5	88.4	Maputo
Marromeu-Gorongosa	132,058.9	0.17	14,270.7	5828.7	111,959.4	84.8	Chimanimani, Marromeu & Gorongosa
Niassa	271,641.0	0.34	45,191.6	45,379.9	181,069.5	66.7	Niassa & Querimbas
Gilé	76,606.4	0.10	25,695.9	2861.1	48,049.4	62.7	Gilé

clearly associated with precipitation, temperature and altitude. Most of the identified zooregions in Mozambique are unprotected, and therefore, represent a great potential for the extension of biodiversity conservation areas in the country. It is critical that most of the zooregions delimited in the present study should be proclaimed biodiversity conservation areas, especially in relatively small zooregions such as the identified Maputo zooregion.

AUTHOR CONTRIBUTIONS

Carlos M. Bento participated in the collection and analysis of data, and in drafting the manuscript. Paulo E. Cardoso participated in data analysis, interpretation and the preparation of illustrations and drafting of the manuscript. Richard D. Beilfuss provided historical data and edited draft versions of the manuscript. Christian T. Chimimba supervised the research project, data analysis and edited draft versions of the manuscript. All the authors read and approved the final submitted version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw data and R code are available upon request from the Maputo Natural History Museum, Mozambique.

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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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