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Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa

Neil D. Burgess[a,b,c,*], *Andrew Balmford*[c], *Norbert J. Cordeiro*[d,e,f], *Jon Fjeldså*[g], *Wolfgang Küper*[h], *Carsten Rahbek*[i], *Eric W. Sanderson*[j], *Jörn P.W. Scharlemann*[k], *J. Henning Sommer*[h], *Paul H. Williams*[l]

[a] *WWF-USA Conservation Science Program, 1250 24th St. NW, Washington, DC, USA*
[b] *Conservation and Management of the Eastern Arc Mountain Forests, P.O. Box 289, Morogoro, Tanzania*
[c] *Conservation Science Group, Zoology Department, University of Cambridge, Cambridge, CB2 3EJ, UK*
[d] *Department of Biological Sciences mc066 University of Illinois-Chicago, 845 W. Taylor St, Chicago IL 60607, USA*
[e] *Departments of Botany/Zoology, Field Museum, 601400 South Lake Shore Drive, Chicago, IL 60605, USA*
[f] *Tanzania Wildlife Research Institute, P.O. Box 661, Arusha, Tanzania*
[g] *Zoological Museum, Universitetsparken 15, DK-2100, Copenhagen Ø, Denmark*
[h] *Nees Institute for Biodiversity of Plants, University of Bonn, Germany, Meckenheimer Allee 170, D-53115 Bonn, Germany*
[i] *NSF Center for Macroecology, Institute of Biology, University of Copenhagen, Universitetsparken 15, DK-2100, Copenhagen Ø, Denmark*
[j] *Living Landscapes Program, Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460, USA*
[k] *Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK*
[l] *The Natural History Museum, South Kensington, London, SW7 5BD, UK*

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ABSTRACT

This paper explores whether spatial variation in the biodiversity values of vertebrates and plants (species richness, range-size rarity and number or proportion of IUCN Red Listed threatened species) of three African tropical mountain ranges (Eastern Arc, Albertine Rift and Cameroon-Nigeria mountains within the Biafran Forests and Highlands) co-vary with proxy measures of threat (human population density and human infrastructure). We find that species richness, range-size rarity, and threatened species scores are all significantly higher in these three tropical African mountain ranges than across the rest of sub-Saharan Africa. When compared with the rest of sub-Saharan Africa, human population density is only significantly higher in the Albertine Rift mountains, whereas human infrastructure is only significantly higher in the Albertine Rift and the Cameroon-Nigeria mountains. Statistically there are strong positive correlations between human density and species richness, endemism and density or proportion of threatened species across the three tropical African mountain ranges, and all of sub-Saharan Africa. Kendall partial rank-order correlation shows that across the African tropical mountains human population density, but not human infrastructure, best correlates with biodiversity values. This is not the case across all of sub-Saharan Africa where human density and human infrastructure both correlate almost equally well with biodiversity values. The primary conservation challenge in the African tropical mountains is a fairly dense and poor rural population that is reliant on farming for their livelihood. Conservation strategies have

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[*] *Corresponding author:* Address: WWF-USA Conservation Science Program, 1250 24th St. NW, Washington, DC, USA. Tel./fax: +1 255 23 261 3082.

E-mail address: neil.burgess@wwfus.org (N.D. Burgess).

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to address agricultural production and expansion, in some cases across the boundaries and into existing reserves. Strategies also have to maintain, or finalise, an adequate protected area network. Such strategies cannot be implemented in conflict with the local population, but have to find ways to provide benefits to the people living adjacent to the remaining forested areas, in return for their assistance in conserving the forest habitats, their biodiversity, and their ecosystem functions.

1. Introduction

One of the most important challenges facing conservation biologists is the conflict of land use within areas that possess globally significant species diversity, because the same areas are generally also favoured by people (Fjeldså and Rahbek, 1998; Balmford et al., 2001a,b; Küper et al., 2004; Luck et al., 2004). This challenge is predicted to result in numerous species extinctions within small areas of the tropics in the coming decades (Brooks et al., 2002; Ricketts et al., 2005). As an example, more than 450 vertebrate species on mainland sub-Saharan Africa are threatened with extinction, including 53 that are gravely threatened and survive at single sites dominated by human presence (Ricketts et al., 2005). Understanding these threats in relation to geographical features, such as mountain or highland relief, may aid in identifying conservation strategies suitable for the biodiversity as well as the human communities of specific types of terrain.

Following the theme of this Special Issue, derived from a Society for Conservation Biology African Section symposium in 2004, we have investigated correlations between biodiversity value and threat in three high biodiversity African tropical mountain systems. These are the Eastern Arc Mountain range of eastern Africa (mainly Tanzania) (Burgess et al., 2007), the Albertine Rift of central Africa (Plumptre et al., 2007), and the Cameroon-Nigeria mountains which form part of the Biafran Forests and Highlands (Bergl et al., 2007). The paper has three principal aims. The first is to test if there is a difference in the human density, human infrastructure (i.e. the density of roads, towns, railways, and electricity) or various biodiversity values of the African tropical mountains, when compared to the remainder of sub-Saharan Africa. The second is to examine if there are correlations between human population density or infrastructure patterns and biodiversity values. The third is to determine how well human population density or human infrastructure is associated with the observed patterns of species richness, endemism, or the degree of species threat – particularly in the three tropical mountains presented in this Special Issue. Finally, we discuss what these results mean for conservation on the ground in these tropical mountain ranges.

2. Methods

2.1. Selection of African tropical mountains

The three African tropical mountain regions that are the focus on this paper are the Eastern Arc Mountains, Albertine Rift and the Cameroon-Nigeria mountains that are part of the Biafran Forests and Highlands. These three tropical mountain areas are all globally exceptional in terms of their species richness (Barthlott et al., 1999; Mutke et al., 2001) and, especially, endemism (Lovett and Wasser, 1993; Burgess et al., 1998a; Kier and Barthlott, 2001; Plumptre et al., 2003, 2004; Plumptre et al., 2007; Burgess et al., 2004; Burgess et al., 2007; Mittermeier et al., 2004; Stattersfield et al., 1998; Bergl et al., 2007). They also all have a high degree of threat as measured by numbers of Red Listed threatened species (e.g. BirdLife International, 2000; Brooks et al., 2002; IUCN, 2004; Ricketts et al., 2005), and rates of habitat loss (Scharlemann et al., 2004, 2005; Green et al., 2005).

Experts familiar with each mountain range selected those one-degree grid cells that best covered these areas (Fig. 1). We have used one-degree grid cells (around 110 × 110 km) as the analytical unit because this is the resolution of our biodiversity data. The other surfaces used have been coarsened to match this one-degree resolution.

2.1.1. *Eastern Arc Mountains*

This mountain range covers the ancient crystalline mountains of eastern Africa, primarily in Tanzania, which are under the direct climatic influence of the Indian Ocean (Lovett, 1988). The area has been shown to be an important centre of endemism in Africa for both plants and vertebrates (Lovett, 1988; Lovett and Wasser, 1993; Burgess et al., 1998a; Burgess et al., 2007; Newmark, 2002). Prioritisation exercises have also identified the Eastern Arc as globally important for conservation; either in its own right – for example in the ecoregions analysis of WWF USA (Olson and Dinerstein, 2002; Burgess et al., 2004), or as a part of a broader geographical region – for example in the Endemic Bird Areas analysis of BirdLife International (ICBP, 1992; Stattersfield et al., 1998) and the Biodiversity Hotspots analyses of Conservation International (Mittermeier et al., 1998, 1999, 2004; Myers et al., 2000).

2.1.2. *Albertine Rift*

Mountains within this range cover a mixture of ancient crystalline mountains and young volcanoes along the western margins and parts of the eastern margins of the Great Rift Valley. The region spans the eastern portion of the Democratic Republic of Congo, as well as parts of western Uganda, Burundi, Rwanda and western Tanzania (Plumptre et al., 2003). The Albertine Rift has been shown to be of global importance for the conservation of narrowly endemic birds (Stattersfield et al., 1998) and other elements of vertebrate biodiversity (Plumptre et al., 2003, 2004; Plumptre et al., 2007; Burgess et al., 2004). The area has also been recognized as part of the Eastern Afromontane biodiversity hotspot in the reanalysis

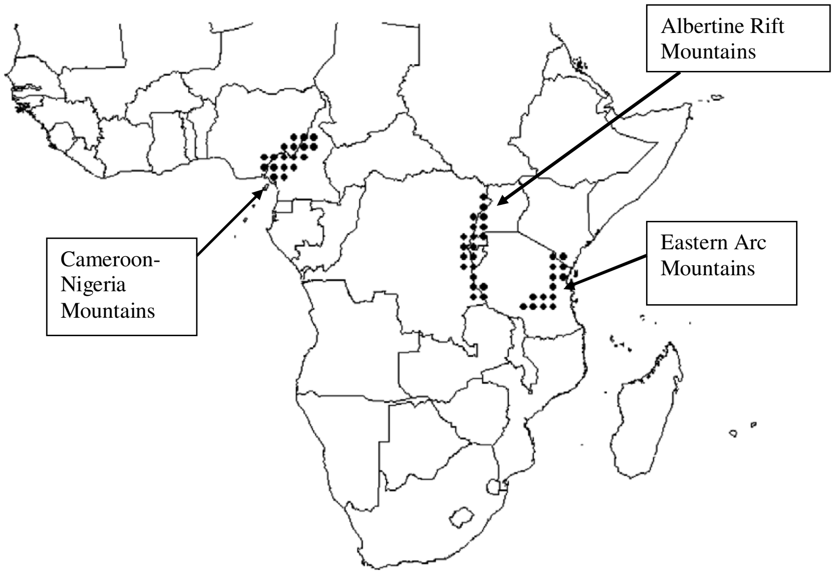


Fig. 1 – Map of sub-Saharan Africa showing the location of one-degree grid cells covering the three high biodiversity tropical mountain ranges in Africa.

of global biodiversity Hotspots by Conservation International (Mittermeier et al., 2004).

2.1.3. *Cameroon-Nigeria mountains*

This mountain range covers a chain of volcanoes of increasing age from the coast towards the interior and is generally located along the border between Nigeria and Cameroon. The Cameroon-Nigeria mountains are of global importance for the conservation of endemic birds (Stattersfield et al., 1998), and for other vertebrates and plants (Burgess et al., 2004; Bergl et al., 2007). This area is part of the larger Guinean Forests of West Africa hotspot identified by Conservation International (Mittermeier et al., 1999, 2004) and is defined by Bergl et al. (2007) as the Biafran Highlands and Forests.

2.2. *Species data*

Vertebrate species data come from the one-degree resolution databases held at the Zoological Museum of the University of Copenhagen (ZMUC) in Denmark (version November 2005). Databases have been extensively updated during 2004 and 2005 to incorporate all known sources of data, and have been recently checked with experts through visits to 8 countries, 12 museums and 25 individuals. For the birds the current database includes distribution maps for 1975 species that have been refined over a period of 10 years using >500 published papers, atlas studies (for 15 African countries), specimen data held at the Zoological Museum in Copenhagen (Denmark), and reliable internet data sources (for example, the Tanzania bird atlas http://tanzaniabirdatlas.com). For mammals, the current database includes distribution maps for 1085 species that have been updated to follow the taxonomy of Wilson and Reeder (2005). Maps are based on data from >1000 published papers and books, and from visits during 2004–2005 to Smithsonian (Washington, DC) and Field Museum of Natural History (Chicago). For amphibians the database includes maps of 739 species that have been based on data in >400 publications, including cross-checking with the online maps of the Global Amphibian Assessment (www.globalamphibians.org) and online taxonomy at Amphibian Species of the World (http://research.amnh.org/herpetology/amphibia). For snakes the database contains distribution records for 467 species that are based on more than 15 years work by the late Jens B. Rasmussen, including visits to more than 20 museums and referring to over 300 published papers. Databases are described in detail elsewhere (Burgess et al., 1998b, 2002a; Brooks et al., 2001; de Klerk et al., 2002a,b, 2004; Fjeldså et al., 1999a, 2004). ZMUC (Denmark) is in the process of preparing all databases, maps and supporting literature for uploading onto the DANBIF internet site (www.danbif.dk).

Plant data are taken form the Biogeographic Information System on African Plant diversity (BISAP), currently hosted at the Nees Institute for Biodiversity of Plants, University of Bonn in Germany. The database version is from November 2005 and contains the point locality data for 5881 species of sub-Saharan African plants (approximately 15% of the estimated total flora for the region), plotted into the one-degree grid cell format. The database was partly based on published monographs for different African plant groups and partly on contributions from different data providers, as detailed elsewhere (Lovett et al., 2000; Bürger, 2001; Kier and Barthlott, 2001; Mutke et al., 2001; La Ferla et al., 2002; Taplin and Lovett, 2003; Küper et al., 2004; Burgess et al., 2005; Barthlott et al., 2005).

Species richness is the number of species per one-degree-grid cell. Range-size rarity was scored as the inverse of each species' range size in sub-Saharan Africa (measured in degree grids), summed for all species in a given grid cell. We also calculate the proportion of red listed species in a one-degree grid cell, in addition to assessing the simple richness of red listed species in each grid cell. The latter is of interest for setting conservation priorities, when the absolute number of threatened species per grid cells needs to be known, whereas the former helps in exploring the drivers of threat.

2.3. Species threat data

We compared the December 2005 version of the IUCN Red List of Threatened species (www.redlist.org; see also IUCN, 2004) against the species lists in our database of vertebrates and produced a threatened species database for all globally-threatened birds, mammals and amphibians combined. Snakes and plants were not addressed as the Red Listing process was incomplete for these taxa and was also biased towards South Africa. Our threatened species database contained 457 vertebrate taxa, with differences between this number and the statistics in the Red List itself arising from taxonomic differences between the two databases, and because we omitted species on the small offshore islands around Africa (Gulf of Guinea Islands, Mafia, Pemba, Zanzibar). As examples of taxonomic differences, in the birds we have not split the Somali thrush *Turdus ludoviciae*, or the Taita Apalis *Apalis fuscigularis*, but we have split the Udzungwa and Rubeho forest partridges *Xenoperdix udzungwensis* and *obscurata*. In the mammals two threatened bat species (*Miniopterus natalensis* and *Scotophilus nucella*) were not mapped in our databases owing to uncertainly over their exact localities. Finally, in the amphibians we regarded *Conraua alleni* as a composite of four species and have mapped all of these as Vulnerable. A full list of the taxa used is available upon request.

2.4. Human population data

Human population data are from the one-degree grid cell resolution version of the Gridded Population of the World (GPW) version 2, compiled at the University of Maryland in the USA (CIESIN, 2000). These data are based on the human population in 1995 as more recent sources compiled for the whole of Africa were unavailable.

2.5. Human infrastructure data

Human infrastructure data are from the Human Footprint developed by the Living Landscapes Program of the Wildlife Conservation Society in the USA (available at http://www.ciesin.org/wild_places). The original human footprint index was mapped at 1-km resolution across the world and was a composite of human population and infrastructure data (Sanderson et al., 2002). In order to derive an index that was independent of human population density, WCS removed the human population layers to produce 'human footprint minus human population'. The resulting index of human infrastructure for the period 1990–1995 includes contributions from human land use (urban and agriculture classes from the Global Land Cover Characterization (Loveland et al., 2000), human infrastructure and access (settlements, roads, railways and water access by large rivers and the ocean, using the VMAP0 datasets (NIMA, 1997)), and human technology (based on the nighttime lights dataset (Elvidge et al., 1997). The original data were provided at a resolution of 1 km grid-cells, and these were coarsened to fit within our 1-degree cells by WCS. For further details of the original dataset see Sanderson et al. (2002).

2.6. Analyses performed

The first step in the analysis was to define a common set of grids that contain data for all the different sources. The bird, mammal, amphibian, snake (our vertebrate database), the 15% sample of plants dataset, and the human population and human infrastructure databases were screened and all grid cells with zero values in any dataset were rejected from all datasets. This procedure resulted in rejecting 354 grid cells (out of 2169) and provided a standardised dataset on 1815 grid cells for further analysis.

Using the standardised dataset, we first tested whether those one-degree grid cells covering African tropical mountains are different in terms of species richness, range-size rarity, species threat, human population density or human infrastructure scores compared to sub-Saharan Africa. To address this we compared mean scores for these different attributes across the 52 tropical mountain grids with the mean scores ±95% confidence intervals for the same number of cells drawn 1000 times at random from across Sub-Saharan Africa (including the 52 mountain grids). The same randomization tests were then undertaken for each of the three mountain ranges separately (Eastern Arc, Albertine Rift, Cameroon-Nigeria mountains).

Second, we investigated correlations between our various biodiversity measures (species richness, range-size rarity, and the number and proportion of threatened species) for vertebrates, richness and range rarity for plants, and human population density or human infrastructure. Our particular interest was where the 52 mountain grid cells fell within the broader set of African cells. Correlations were inspected visually using $\log_{10}$-transformed data and analysed statistically using Kendall rank-order correlations on the untransformed data (we used this method instead of Spearman rank-order correlations because we were also interested in partial correlations - see below).

Third, we assessed whether human population or human infrastructure was the better correlate with species richness, range-size rarity, or the number or proportion of threatened species in one-degree grid cells. These tests were performed on the data from the three high biodiversity tropical mountains, and on all grid cells across sub-Saharan Africa. Kendall partial rank-order correlations were used to test for significance of the relationship between biodiversity and human density or infrastructure.

Mapping was completed within Worldmap (Williams, 1998), graphs within MS Excel, Kendall rank-order correlations within SPSS (SPSS Inc., Chicago, IL, v. 11.5), and Kendall partial rank-order correlations (Siegel and Castellan, 1988) and randomization tests in S-Plus (Insightful, Seattle, Washington, v. 6.0). Spatial autocorrelation between scores for nearby cells means that the degrees of freedom in the correlations presented here (but not the correlation coefficients) are exaggerated; consequently, we do not present *p*-values for the Kendall rank-order or partial rank-order tests.

2.7. *Methodological and data challenges*

Biogeographical analyses have a number of challenges, not least that they are limited by the availability of data, which is certainly not yet comprehensive across Africa (e.g. Küper et al., 2006; Butchart et al., 2005). For this reason, continent-wide data must necessarily be rather coarse and we therefore concentrate our efforts in understanding large-scale patterns.

The information underlying the species databases differs slightly across taxa. Vertebrate distributions are based on records but the majority of taxa have interpolated ranges based on expert knowledge. Species range sizes tend to be under-documented in remote areas, whereas documentation tends to be better in more accessible areas. The plant distributions only include documented collection localities. This is also the case for the poorly known species of amphibians and snakes, and some mammals (for example bats). For those species mapped without interpolation, the data are generally more precise, but less accurate as they suffer more from collection and access biases. The difference between interpolated data and documented occurrences is stronger when comparing patterns of range-size rarity (see below), as range sizes tend to be generally larger in interpolated data. In this regard, the bird and part of the mammal data are more complete and may provide a realistic picture of true patterns than the other taxonomic groups.

In the plant database, sub-Saharan plant diversity is represented through a sub-sample of the flora (about 15% of the species). Sampling tends to be more intense in easily-accessible areas (for details, see Küper et al., 2006), but this is also true of all other taxon-based diversity maps and indices based on only partial data (Butchart et al., 2005), and there are no methods to systematically address this issue.

We have retained coastal cells even though their area of land is not the same as mainland cells. If there was a general correlation between biodiversity and threat, then our assumption is that biodiversity and threat in these coastal cells will be affected by area in similar ways, thus making no difference to our overall results (for discussion also see Rahbek and Graves, 2000; Rahbek and Graves, 2001). Data from each one-degree grid cell were also not corrected for variations in surface area (due to topography). This is because an unpublished analysis using South American bird data showed no differences in the results obtained, regardless of whether analyses were undertaken on uncorrected one-degree grid units, or ones that had been corrected to their 3-dimensional surface area (Rahbek et al., unpublished data).

3. Results

3.1. *Are the African tropical mountains different to the rest of Africa?*

3.1.1. *Human population density*

Looking at the three African tropical mountain regions in combination, their overall human population density (58.7 persons per square kilometer) is more than double the mean score for sub-Saharan Africa (24.7 persons per square kilometer; Table 1). However, when making the same comparison by individual mountain blocks, the difference was significant only for the Albertine Rift (Table 2).

3.1.2. *Human infrastructure*

Small but significant differences were found in the mean human infrastructure scores of the three high biodiversity mountains and the whole of sub-Saharan Africa (Table 1). For the Eastern Arc the differences were not significant, but the Albertine Rift and Cameroon-Nigeria mountains had significantly higher levels of infrastructure compared to sub-Saharan Africa (Table 2).

3.1.3. *Species richness of plants and vertebrates*

Mean species richness scores for plants and vertebrates in the three high biodiversity tropical mountain regions were about

Table 1 – Mean (±SD) species richness, range-size rarity, number of threatened species, proportion of threatened species, human population density and human infrastructure of one-degree grid cells across Sub-Saharan Africa (*n* = 1815 one-degree grid cells) and those of the combined grid cells of the high biodiversity tropical mountains (*n* = 52) of the Eastern Arc Mountains, Albertine Rift and Cameroon-Nigeria mountains

Attribute	All Sub-Saharan Africa (*n* = 1815)		All high biodiversity tropical mountains (*n* = 52)					
	Mean	SD	Mean	SD	Mean random	Lower 95%	Upper 95%	P
Species richness (vertebrates) *n* = 3957	376.1	169.9	662.9	142.2	375.7	329.5	421.1	<0.002
Range-size rarity (vertebrates) *n* = 3957	2.1	2.6	10.5	7.7	2.1	1.5	3.0	<0.002
Species richness (plants) *n* = 5881	47.3	65.4	33.3	85.9	47.4	32.2	65.8	<0.002
Range-size rarity (plants) *n* = 5881	3.2	9.2	11.1	10.1	3.2	1.5	6.3	<0.002
Threatened birds, mammals, amphibians (*n* = 457)	7.1	6.8	26.6	18.0	7.1	5.5	9.3	<0.002
Proportion threatened vertebrates (threatened species/total vertebrates)	0.022	0.018	0.038	0.022	0.022	0.017	0.027	<0.002
Human population density (people per square km)	24.7	49.8	58.7	66.9	24.5	14.2	39.4	<0.002
Human infrastructure index (see text)	10.5	4.9	12.9	3.3	10.5	9.1	11.8	<0.002

Randomisation tests (with upper and lower 95% confidence limits and significance values (P)) indicate whether species, human population density and human infrastructure values of the mountains were significantly different from those of all sub-Saharan Africa.

Table 2 – Mean (±SD) species richness, range-size rarity, number of threatened species, proportion of threatened species, human population density and human infrastructure of one-degree grid cells in the high biodiversity tropical mountains of the Eastern Arc Mountains ($n = 14$ one-degree grid cells), Albertine Rift ($n = 20$) and Cameroon-Nigeria mountains ($n = 18$)

Attribute	Eastern Arc ($n = 14$ grid cells)						Albertine Rift ($n = 20$ grid cells)						Cameroon Nigeria mountains ($n = 18$ grid cells)					
	Mean	SD	Mean-random	lower 95%	Upper 95%	P	Mean	SD	Mean-random	Lower 95%	Upper 95%	P	Mean	SD	Mean-random	Lower 95%	Upper 95%	P
Species richness (vertebrates) $n = 3957$	**693.6**	69.0	374.9	287.6	461.5	<0.002	**745.7**	135.3	376.2	304.4	456.3	<0.002	**547.0**	116.1	375.9	291.6	454.0	<0.002
Range-size rarity (vertebrates) $n = 3957$	**12.8**	6.1	2.1	1.2	4.0	<0.002	**10.0**	6.1	2.1	1.3	3.5	<0.002	**9.4**	10.1	2.1	1.2	3.6	<0.002
Species richness (plants) $n = 5881$	**152.9**	60.4	45.9	19.6	86.7	<0.002	**127.7**	67.3	47.8	24.5	80.4	<0.002	**124.4**	117.7	47.4	22.9	86.4	<0.002
Range-size rarity (plants) $n = 5881$	**18.3**	11.3	3.1	0.8	9.9	<0.002	9.7	7.4	3.4	1.0	9.9	0.058	7.1	9.3	3.3	1.0	9.6	0.098
Threatened birds, mammals, amphibians ($n = 457$)	**28.7**	14.7	7.1	4.6	11.3	<0.002	**25.1**	16.0	7.0	4.9	10.5	<0.002	**26.6**	22.7	7.1	4.8	11.2	<0.002
Proportion threatened vertebrates (threatened species/ total vertebrates)	**0.041**	0.019	0.022	0.014	0.032	<0.004	**0.032**	0.017	0.022	0.015	0.031	0.042	**0.043**	0.028	0.022	0.015	0.032	<0.002
Human population density (people per square km)	29.9	21.3	24.9	8.0	59.2	0.53	**94.6**	90.3	24.2	9.8	50.6	<0.002	41.2	38.0	24.2	9.7	58.7	0.168
Human infrastructure index (see text)	10.7	3.4	10.5	7.8	13.1	0.84	**12.8**	2.8	10.5	8.1	12.6	0.044	**14.8**	2.8	10.4	8.3	12.7	<0.002

Randomisation tests (with upper and lower 95% confidence limits and statistical significance (P) values) indicate whether biodiversity values and human population and infrastructure of each mountain range were significantly different from those of all sub-Saharan Africa. Significant tests are shown in bold.

double those of the remainder of sub-Saharan Africa (Table 1). Random selection of one-degree grid cells from the database on vertebrates showed that the Albertine Rift, Eastern Arc Mountains and Cameroon-Nigeria mountains had significantly higher vertebrate or plant species richness than a sample of grids throughout Africa (Table 2).

3.1.4. *Range-size rarity of vertebrates and plants*

Mean range-size rarity scores for both vertebrates and the sample of plants were around three times higher on the tropical mountains when compared to mean scores across all of sub-Saharan Africa (Table 1). Random selection of one-degree grid cells from the vertebrate database showed that the Albertine Rift had significantly higher vertebrate range-size rarity than a sample of grids throughout sub-Saharan Africa, and the same was true for the Cameroon-Nigeria mountains and the Eastern Arc Mountains. For the sample of plants only the Eastern Arc mountain grid cells had significantly higher range-size rarity than all grid cells from sub-Saharan Africa; the trend towards higher plant range-size rarity on mountains was only marginal for the Albertine Rift and Cameroon-Nigeria mountains (Table 2).

3.1.5. *Threatened vertebrates*

Mean numbers of threatened species (birds, mammals and amphibians) are more than four times higher in the African tropical mountains than across all of sub-Saharan Africa (Table 1). All three tropical mountain regions have significantly more threatened vertebrates than sub-Saharan Africa (Table 2). In terms of the proportion of threatened vertebrates per grid cell, all three tropical mountain regions also have a significantly higher proportion of threatened vertebrates than Sub-Saharan Africa (Table 2).

3.2. *Are biological attributes across sub-Saharan Africa and the African tropical mountains correlated with human population density?*

3.2.1. *Species richness*

Across sub-Saharan Africa there was a strong positive correlation at this spatial scale between human population density and species richness of vertebrates (Kendall's $\tau = 0.33$, $n = 1815$; Fig. 2a). The same holds true for the sample of plants (Kendall's $\tau = 0.32$, $n = 1815$; Fig. 2b). The 52 one-degree grid cells corresponding to the Eastern Arc, Albertine Rift and Cameroon-Nigeria mountains are located at the top right hand section of scatter plot graphs of species richness and human population density (Fig. 2a,b). Within the African tropical mountains there was a strong correlation between human population density and species richness for both vertebrates ($\tau = 0.45$, $n = 52$) and the sample of plants ($\tau = 0.39$).

3.2.2. *Range-size rarity*

Across sub-Saharan Africa there was a strong positive correlation between human population density and range-size rarity scores for vertebrates (Kendall's $\tau = 0.30$, $n = 1815$, Fig. 2c). This correlation was present, but weaker, for our sample of plants ($\tau = 0.24$, $n = 1815$; Fig. 2d). The 52 one-degree grid cells of the Eastern Arc, Albertine Rift and Cameroon-Nigeria Mountain cells fall in the top right-hand portion of graphs plotting range-size rarity against human population density (Fig. 2c,d), meaning they have both high range-size rarity scores and high human population density. Within the tropical mountain grids there was a significant correlation between the human population density and range-size rarity scores for vertebrates ($\tau = 0.28$, $n = 52$) and the sample of plants ($\tau = 0.27$).

3.2.3. *Threatened species*

A positive correlation was found between the number of threatened species and human population density across sub-Saharan Africa (Kendall's $\tau = 0.20$, $n = 1815$). However, when looked at as the proportion of threatened vertebrates (bird, mammal and amphibian) species per cell against human population density, the correlation was negative ($\tau = -0.12$, $n = 1815$). The 52 one-degree grid cells of the African tropical mountains fall in the top right-hand portion of graphs plotting number of threatened species against human population density (Fig. 2e), and there was a positive correlation between human population density and the number of threatened vertebrate species ($\tau = 0.33$, $n = 52$).

3.3. *Are biological attributes across sub-Saharan Africa and the African tropical mountains correlated with human infrastructure?*

3.3.1. *Species richness*

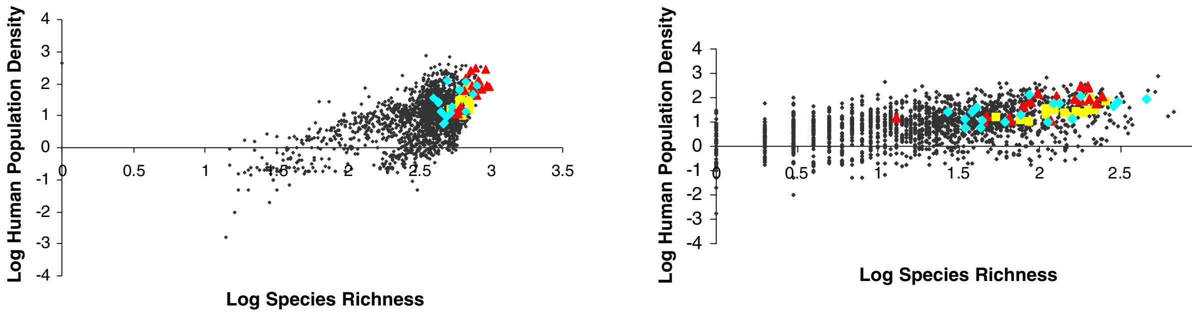
Across sub-Saharan Africa species richness of vertebrates and human infrastructure was positively correlated (Kendall's $\tau = 0.28$, $n = 1815$), as was plant richness and human infrastructure ($\tau = 0.30$, $n = 1815$). The one-degree grid cells corresponding to the three tropical mountain ecoregions were all located in the top right portion of the graphs between these variables – for both vertebrates (Fig. 3a) and plants (Fig. 3b). Within the tropical African mountains there was a positive correlation between the human infrastructure and range-size rarity scores for the sample of plants ($\tau = 0.20$, $n = 52$), but this was weaker for vertebrates ($\tau = 0.11$, $n = 52$).

3.3.2. *Range-size rarity of vertebrates and plants*

Across sub-Saharan Africa there was a positive correlation between human infrastructure and range-size rarity scores for vertebrates (Kendall's $\tau = 0.28$, $n = 1815$), and weaker one between human infrastructure and range-size rarity for our sample of plants ($\tau = 0.24$, $n = 1815$). The one-degree grid cells corresponding to the three tropical mountains are located towards the right hand end of plots between these variables, but there are grid cells with higher human infrastructure and the same range-size rarity scores (Fig. 3c,d). There was no correlation between human infrastructure and range-size rarity in the African tropical mountains for either vertebrates ($\tau = 0.12$, $n = 52$) or the sample of plants ($\tau = 0.08$, $n = 52$).

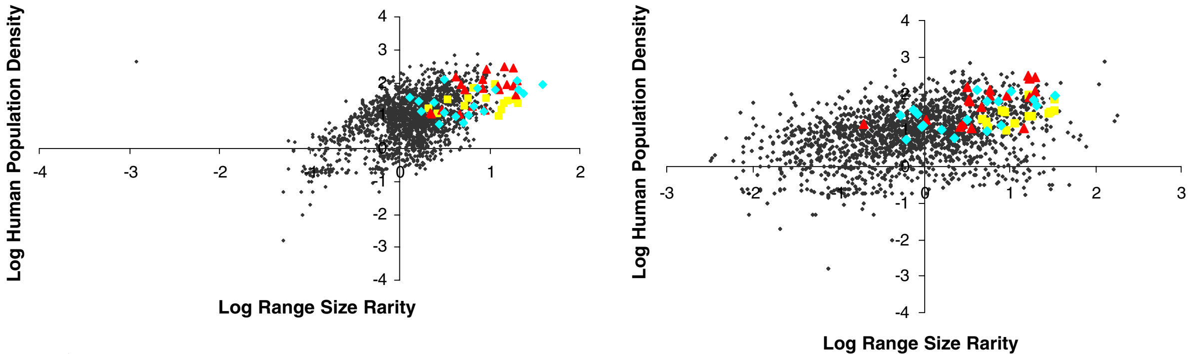
3.3.3. *Threatened vertebrates*

There was a weak positive correlation between the number of threatened vertebrates and human sub-Saharan Africa infrastructure (Kendall $\tau = 0.16$, $n = 1815$). However, when converted to a proportion of threatened species, the correlation was weaker and negative ($\tau = -0.14$, $n = 1815$). The African tropical mountains are located towards the top right-hand



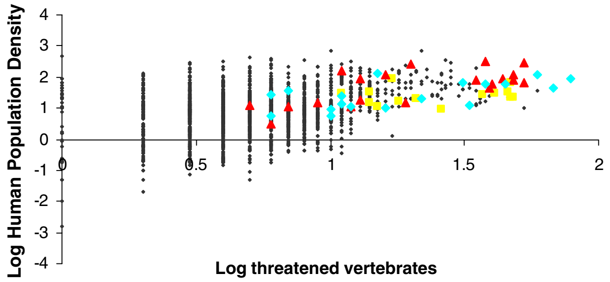
a) Vertebrates

b) Plants



c) Vertebrates

d) Plants



e) Threatened Vertebrates

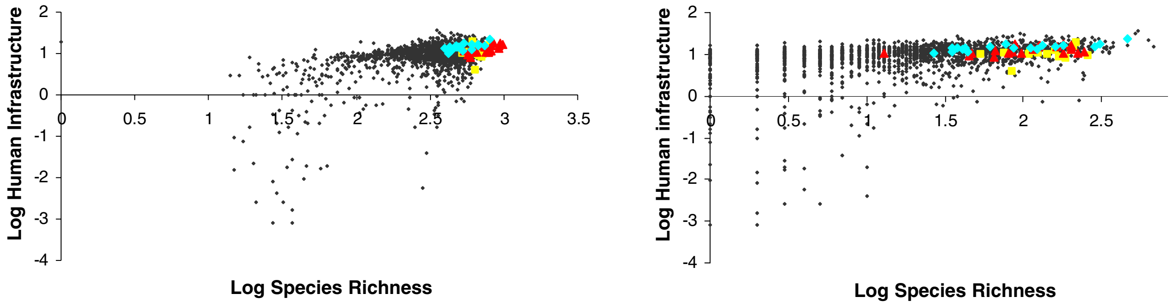
Fig. 2 – Scatter plots of species richness, range-size rarity and threatened species of vertebrate animals and plants against human population density across 1815 one-degree grid cells in sub-Saharan Africa. (a) Log vertebrate species richness against log human population density. (b) Log plant species richness against log human population density. (c) Log vertebrate range-size rarity against log human population density. (d) Log plant range-size rarity against log human population density. (e) Log bird, mammal, amphibian threatened species against log human population density. Yellow squares = Eastern Arc Mountains, Red triangles = Albertine Rift mountains, Blue diamonds = Cameroon-Nigeria mountains.

part of the graph between human infrastructure and number of threatened species (Fig. 3e), but there was only a weak correlation between these two variables (Kendall $\tau = 0.15$, $n = 52$).

3.4. *Partial correlations of human population density and infrastructure with biodiversity measures*

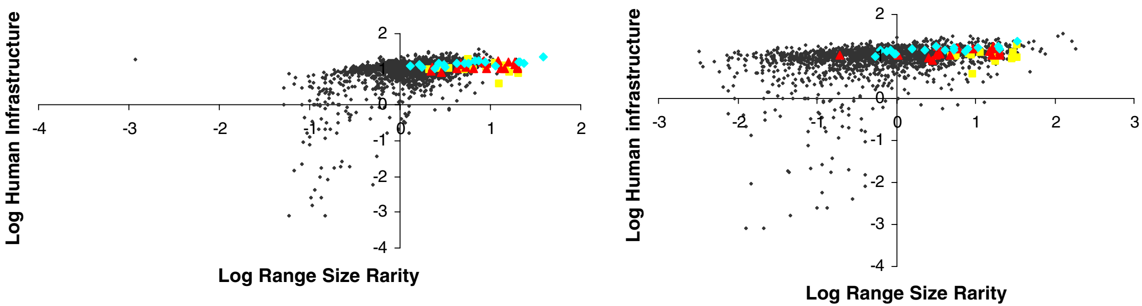
Kendall partial rank-order correlations were used to determine whether biodiversity values were better correlated with human population density or human infrastructure, particularly on the high biodiversity tropical mountains. These tests showed that population density was a better correlate with biodiversity values in the African tropical mountains than human infrastructure (Table 3). Across all of sub-Saharan Africa human population density and human infrastructure were both good correlates with species richness and range-size rarity scores of vertebrates and plants (Table 3). In general population density was a marginally better correlate than infrastructure with the various biodiversity values, except for the proportion of threatened vertebrates, which was slightly better correlated with human infrastructure (Table 3).

It is conceivable that for some taxa these results are driven in part by sampling effects. For example, those datasets based on distribution records rather than interpolated ranges (mainly plants, but also amphibians and reptiles) may, to some extent, be biased by greater sampling effort in areas that are more accessible because they have better infrastructure. However, even for these taxa, their scores are slightly more strongly correlated with human population density than with infrastructure. This holds true as well when the



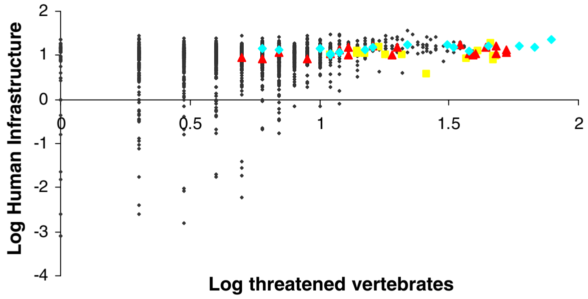
a) Vertebrates

b) Plants



c) Vertebrates

d) Plants



e) Threatened vertebrates

Fig. 3 – Scatter plots of species richness and range-size rarity of vertebrate animals and plants against human infrastructure across 1815 one-degree grid cells in sub-Saharan Africa. (a) Log vertebrate species richness against Log human infrastructure. (b) Log plant richness against Log human infrastructure. (c) Log vertebrate range-size rarity against Log human infrastructure. (d) Log plant range-size rarity against Log human infrastructure. (e) Log number of threatened vertebrates against Log human infrastructure. Yellow squares = Eastern Arc Mountains, Red triangles = Albertine Rift mountains, Blue diamonds = Cameroon-Nigeria mountains.

analysis is repeated with plant diversity maps derived from bioclimatic modeling, which are much more independent of the locations of collection sites (Küper and Sommer, unpublished analysis).

4. Discussion

Using fully updated datasets for birds, mammals, amphibians, snakes and a 15% sample of vascular plants we show that the three high biodiversity tropical mountain ranges of Africa have higher species richness, range-size rarity (endemism) and number of threatened species than the overall mean across sub-Saharan Africa. For both plants and animals, the mean one-degree species-richness scores in the tropical mountains are about double those for the whole of sub-Saharan Africa, three times higher for range-size rarity and four times higher for number of threatened species.

In terms of factors that threaten biodiversity, all mountains also have a higher density of people than the mean for sub-Saharan Africa of 25 people per square kilometer, but densities are significantly higher only in the Albertine Rift. All mountains also have higher levels of infrastructure development than the mean across sub-Saharan Africa – a difference that is significant in the Albertine Rift and the Cameroon-Nigeria mountains. Overall, human population density is more highly associated with the biodiversity values of the three African tropical mountain regions than is human infrastructure. Across sub-Saharan Africa human density and infrastructure are almost equally associated with biodiversity value. However, at local scales, human population centres are

Table 3 – Kendall partial rank-order correlations between biodiversity values (vertebrates and plants) and human population density and Human infrastructure across sub-Saharan Africa

Variable 1	Variable 2	Partialled out variable	All Sub-Saharan Africa		African tropical mountains	
			T	z	T	z
Species richness (vertebrates)	Human population	Human infrastructure	**0.245**	15.63	**0.435**	4.55
	Human infrastructure	Human population	**0.161**	10.28	0.034	0.35
Species richness (plants)	Human population	Human infrastructure	**0.228**	14.58	**0.365**	3.82
	Human infrastructure	Human population	**0.192**	12.27	0.141	1.47
Range-size rarity (vertebrates)	Human population	Human infrastructure	**0.215**	13.74	**0.264**	2.76
	Human infrastructure	Human population	**0.172**	10.95	0.072	0.75
Range-size rarity (plants)	Human population	Human infrastructure	**0.162**	10.35	**0.255**	2.67
	Human infrastructure	Human population	**0.160**	10.19	0.031	0.33
Threatened vertebrates	Human population	Human infrastructure	**0.153**	9.75	**0.316**	3.30
	Human infrastructure	Human population	**0.079**	5.07	0.090	0.94
Proportion of threatened vertebrates	Human population	Human infrastructure	**−0.067**	−4.27	**0.207**	2.16
	Human infrastructure	Human population	**−0.099**	−6.32	0.062	0.65

Tests based on data from 1815 one-degree grid cells. Significant results are in bold.

located inside broader areas that are biologically rich (e.g. McNeilage et al., 1998; Plumptre, 2002; Plumptre et al., 2007). A more detailed discussion of these findings is presented below.

4.1. *How do these results compare with conservation prioritization assessments?*

Our results support those of various conservation organisations that have looked at threat as a factor in the ranking of areas for conservation attention. For example, BirdLife International (Stattersfield et al., 1998) ranked its Endemic Bird Areas (EBAs) in terms of threat and identified our three focal mountain areas as regions of potentially high conflict between people and biodiversity. Further work on this issue has shown that EBAs have more agriculture than other parts of the globe and in the more converted EBAs there are more threatened species of birds (Scharlemann et al., 2004). Similarly, although the first 'Biodiversity Hotspots' analysis of Conservation International (Mittermeier et al., 1999) did not recognize the Albertine Rift (see also Küper et al., 2004), the 'Hotspots Revisited' analysis did identify this region as a center of endemism and threat, forming a part of the newly-defined Eastern Afromontane Hotspot (Mittermeier et al., 2004). The same areas were identified in the original 'Global 200' analysis of priority ecoregions by WWF-USA (Olson and Dinerstein, 2002; Kier et al., 2005), and in the update of that analysis (Burgess et al., 2004). In analyses that look broadly across the world, regions of high human density also show high rates of habitat loss and hence potential conflicts between people and biodiversity conservation (Balmford and Long, 1994; Cincotta et al., 2000; Brooks et al., 2002; Scharlemann et al., 2004, 2005; Green et al., 2005).

Previous work has also suggested that the high biodiversity values of tropical mountains and associated high human population densities were due to the long term climatic stability of these areas (Fjeldså et al., 1997, 1999b; Fjeldså, in press). The high biodiversity values of these areas also correlated with high human linguistic richness (Moore et al., 2002; Manne, 2003). African biodiversity patterns are influenced by the geological history and the current geomorphology of the African continent (Jetz and Rahbek, 2002; Jetz et al., 2004), and rapid change of the current landscape through increased human population density and infrastructure has the potential to rapidly erode cultural and biological values of the three mountain ranges chosen as the foci of this paper.

4.2. *How do these results inform the debate on conservation challenges in the African tropical mountains?*

Tropical African mountains support many rural people because they have better climates (wetter and/or more reliable seasons) than surrounding lowland areas, and thus permit the establishment of permanent agricultural systems (Blyth et al., 2002). All three of the mountains considered here have higher than the overall sub-Saharan African average human population densities, with the Albertine Rift having more than three times as many people per unit area as that, and the Cameroon-Nigeria mountains having almost double. Only the Eastern Arc Mountains have close to the sub-Saharan African average density, but even there human densities are higher in the mountains than in the surrounding lowlands. Compared with developed countries, all three of the African tropical mountains have low human infrastructure development, but all three mountains have higher infrastructure than average for Africa. The fact that the Eastern Arc has relatively low infrastructure scores is linked to the relatively lower human population density than in the other mountains and because they are located in two of the poorest countries in the world. A primary conservation challenge in the African tropical mountains is therefore finding solutions to the livelihood needs of dense rural populations that are dependent on agriculture, but still suffer from poor human infrastructure and high levels of poverty.

Farmland expansion in developing countries exerts a significant pressure on the survival of threatened vertebrates, such as birds (Green et al., 2005). In the African tropical mountains human pressure for farmland extends right to the boundaries of most reserves, and into many of them (Burgess et al., 2002b; Plumptre et al., 2004). The pressure to expand farmland areas comes from an increasing rural population and from poor agricultural systems that do not retain soil fertility, despite the existence of agricultural innovations that can solve this problem (e.g. Tiffen et al., 1994). Innovations may require suitable property right systems and close links with external markets to provide a stable income (Beaumont and Walker, 1996). This is rarely the case in the montane areas, where there is instead a continuous pressure for 'new' farmland as existing farmed areas decline in productivity. The main driver of biodiversity loss is therefore the transformation of more natural habitats to agriculturally used land (Geist and Lambin, 2002; Chazdon, 2003; MEA, 2005), and globally, most of the remaining suitable and as yet unconverted land is located in Africa. The increasing demand for food by growing human populations is projected to further enhance this pressure, underlining the need of improved land use practices and technologies to enhance yield (Balmford et al., 2005; Mooney et al., 2005) in parallel with the inevitable acquisition of further areas of land for agriculture.

Another conservation challenge is that most of the forest habitats in the three tropical mountain ranges exist inside areas protected either by government management authorities (mainly in the Eastern Arc and Albertine Rift), or local communities (mainly in the Cameroon-Nigeria mountains). The government agencies are often underfunded and struggle to conserve the areas they have under their control (e.g. Burgess et al., 2007). Local communities may require fewer resources for management as they are living in the areas concerned, but if they are to be involved in forest management they require defined benefits to compensate for their time input. In the African tropical mountains a number of large-scale conservation strategies have been developed, or are under development. In the Albertine Rift a group of NGOs has developed a conservation vision and action plan (www.panda.org), which is now under implementation. A similar process in Tanzania, supported by UNDP–GEF is also aiming to develop a conservation strategy by the end of 2006 (www.easternarc.or.tz). There is no overall conservation strategy for the Cameroon-Nigeria mountains that make up the Biafran Forests and Highlands. These strategies are supplementing species-oriented conservation, mainly in parks and reserves, with function-oriented conservation of ecosystem services essential for human livelihoods (Daily, 1997; United Nations, 2000; Scholes and Biggs, 2004). This has to be done in a participatory way by taking into consideration the interests and needs of the local population as well as the responsibilities of more distant stakeholders. The resulting integrated conservation strategies may deviate somewhat from solely biodiversity-centred conservation targets, but may be more locally appropriate and possible to implement under developing country conditions (Wells and McShane, 2004).

4.3. *Caveats and research needs*

As with all similar studies looking at biodiversity patterns, and correlations with other attributes of, for example, threat, the results are only as reliable as the data underlying them. This paper is no exception and there are a number of issues we feel need to be discussed. For example, the human population data are from 1995, and there has been a significant movement of people to cities since that time, and wars have also caused significant population movements in some countries, particularly the Albertine Rift region (see Kanyamibwa, 1998). Human infrastructure data also relate to the 1990s. More recent data, compiled for the whole of Africa, are not available and hence whether changes in the past 10 years will have made much difference to the results presented here cannot be easily tested.

For the vertebrate data, although we have worked to gather all the available literature and have developed distribution maps of all species of birds, mammals, amphibians and snakes, we still have not mapped the other species of reptiles. There are several hundred non-snake reptile species within the region and their distributions are often very poorly known. Compiling non-snake reptile data and using them for analysis may change the results we get here – not least because reptiles are able to tolerate drier habitats than many vertebrates and patterns of richness and endemism might shift towards drier regions.

For the plant data, we still only have a sample of the African species mapped, and some of these maps are not verified or closely checked. They are mainly based on published monographs. As a consequence, our analyses concerning plants should be treated with more caution than those for the vertebrates. Mapping African plants is a 'work in progress' and we hope that additional sources are made available for analysis over the coming years. This will entail a huge effort as many of the species are only known from a few specimens from accessible sites – and thus their true ranges are not clear.

At the one-degree resolution of analysis, we cannot be certain that the biodiversity or human population or human infrastructure data are actually overlapping at finer spatial resolutions. It is possible that high human density in one part of the grid cell does not correspond with high species diversity in the same part of the grid cell. In fact these attributes might be as much as 100 km apart and they would still fall within the same grid cell. There are thus evident limits on what the one-degree scale of analysis can really tell about contiguity of these attributes. In a related point our degradation of the human population and human infrastructure data to the one-degree cell format has resulted in a significant loss of information that would be relevant for detailed conservation planning. The resolution of the biodiversity data used here does not allow finer scale issues to be investigated.

Evidently, there is still much work to be done to develop datasets on many different aspects of African human and biological life. This will take time and further resources. Nevertheless, great progress has been made, and continues to be made in pulling together what is already known, and field work and other studies add to this body of knowledge every year. The conclusions presented in this paper can be repeated when these new sources of information are available, but we suspect that the patterns are robust and will remain, even after the addition of newly acquired data.

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