BIODIVERSITY RESEARCH

Targeted vertebrate surveys enhance the faunal importance and improve explanatory models within the Eastern Arc Mountains of Kenya and Tanzania

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ABSTRACT

Aim Detailed knowledge of species distributions, endemism patterns and threats is critical to site prioritization and conservation planning. However, data from biodiversity inventories are still limited, especially for tropical forests, and even well recognized hotspots remain understudied. We provide an example of how updated knowledge on species occurrence from strategically directed biodiversity surveys can change knowledge on perceived biodiversity importance, and facilitate understanding diversity patterns and the delivery of conservation recommendations.

Location Eastern Arc Mountains (EAM), Kenya and Tanzania.

Methods We surveyed amphibians, reptiles, birds and mammals during 2005–2009, targeting mountain blocks that had been poorly surveyed or unsurveyed by the early Noughties. We combined new and old data to produce a database of species presence by mountain block spanning four decades of research. Species richness is regressed against survey effort, funding, ecological and human disturbance factors to analyse the best predictors of vertebrate richness across mountain blocks. Similarity among species assemblages among blocks is analysed using dissimilarity analysis.

Results New surveys raised the number of endemic and regional endemic vertebrates by 24% (from 170 to 211 species), including 27 new species of which 23 are amphibians and reptiles. Vertebrate richness is best explained by forest area, but rainfall is also important, especially for amphibians and reptiles. Forest elevational range is important for mammals and for block-endemic birds. Funding explains 19% of the variation in total species richness, while survey effort generally explains < 10% of variance. Cluster analysis shows that species assemblages are partitioned by geographical proximity among mountain blocks.

Main conclusions The biological value of the EAM has been underestimated, and strategic surveys are important even in well-recognized hotspots. The exceptional and global importance of these mountains for endemic vertebrates is highlighted, supporting the development of a network of Nature Reserves and the proposed inclusion within UNESCO's natural World Heritage Sites.

Keywords
Africa, conservation planning, hotspot, Tanzania, tropical forests, vertebrates.

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INTRODUCTION

While broadscale patterns of terrestrial species richness are best explained by water and energy availability (e.g. Currie, 1991; Hawkins, 2001; Jetz & Fine, 2012), patterns of variation in species richness and endemism at the local and regional scale are less understood and likely driven by complex interactions between past and current ecological and evolutionary processes (Jetz *et al.*, 2004; Orme *et al.*, 2005; Hurlbert & Jetz, 2007; Rahbek *et al.*, 2007; Dimitrov *et al.*, 2012). However, declining funds for basic species inventories and taxonomy hinders the potential for detailed study of the factors underlying biodiversity patterns (Whitehead, 1990; Ahrends *et al.*, 2011a), with the gap in data availability and updates being particularly severe in the tropics (Prance *et al.*, 2000). In addition, funding for biodiversity surveys may be disproportionally allocated to already well-known areas, hence further biasing the apparent importance of these areas (Ahrends *et al.*, 2011b). Given that biodiversity importance is generally measured on species richness, endemism and associated threat status (Brooks *et al.*, 2006; Fritz & Purvis, 2010), a consequence of this data deficit is that conservation efforts may not be based on comprehensive and/or consistent evidence.

Here, we show how updated knowledge on species occurrence from strategically directed biodiversity surveys in a global biodiversity hotspot can considerably change the knowledge on perceived biodiversity, facilitating analysis of diversity patterns and their determinants, and the provision of conservation recommendations. The Eastern Arc Mountains (EAM) of Kenya and Tanzania are an emblematic region for conservation. The area has been long recognized for its outstanding biological importance, especially for forest vertebrates (Burgess *et al.*, 1998, 2007; Newmark, 2002). In early global conservation prioritization analyses, the level of endemism coupled with historical loss of habitat qualified the EAM and the adjacent coastal forests as the biodiversity hotspot with the highest density of endemic vertebrates on earth (Myers *et al.*, 2000). Prior to our study, knowledge on forest vertebrate diversity in the EAM was mainly defined using surveys conducted before 2005 and in a limited number of sites (Burgess *et al.*, 2007; see also Table 1), although there was also a small number of newer taxonomic studies and block-specific checklists for amphibians and reptiles (Menegon *et al.*, 2008, 2011; Loader *et al.*, 2011). Moreover, no comprehensive and predictive analysis of potential drivers of richness and endemism was performed. While recent studies have examined patterns of diversity in plants (Ahrends *et al.*, 2011a,b), estimated plant richness based on inventory data (Platts *et al.*, 2010) and analysed deforestation trends in the EAM (Hall *et al.*, 2009; Platts *et al.*, 2011), there has been no recent analysis of patterns of richness and endemism for forest vertebrates across the EAM.

In our study, we specifically aimed to (1) assess the levels of endemism among mountain blocks using all data, including a large number of new surveys, (2) establish the best predictors of species richness and (3) analyse similarities in species assemblages. Our general underlying hypothesis was that previously undersurveyed blocks are potentially as important as the well-surveyed ones, and, in turn, that new surveys especially completed for poorly known amphibians and reptiles would lead to a consistent change in the known richness and level of endemism for these groups. In addition, we assumed that richness and endemism are positively affected not only by forest area but also by forest elevational range, rainfall and survey effort and negatively affected by proxies of human impact on the forest (i.e. surrounding human density, forest loss, human encroachment). We also discuss our results in the context of listing the EAM under UNESCO's World Heritage Convention (United Republic of Tanzania, 2011; Bertzky *et al.*, 2013; Le Saout *et al.*, 2013) and the recent upgrading of Forest Reserves to Nature Reserves, against actual protection on the ground (e.g. Rovero *et al.*, 2012).

METHODS

Study area

The EAM comprise 13 mountain blocks ranging from southern Kenya to south-central Tanzania (Fig. 1; see Burgess *et al.*, 2007 for details on each block). These mountains

Table 1 The vertebrate species richness in the Eastern Arc Mountains of Kenya and Tanzania grouped by endemism and, in parenthesis, the increase (%) in the number of species relative to the baseline study (Burgess *et al.*, 2007). An index of the survey effort deployed pre- and post-baseline is also given (see Methods for details)

	Mammals	Birds	Reptiles	Amphibians	All
Endemic and regional endemic	25 (8.7)	51 (6.3)	59 (28.3)	76 (43.4)	211 (24.1)
EAM endemic (E)	11 (10.0)	23 (15.0)	42 (44.8)	60 (57.9)	136 (40.2)
Regional endemic (RE)	14 (7.7)	28 (0)	17 (0)	16 (6.7)	75 (2.7)
Single-block endemic (SBE)	5 (0)	11 (0)	19 (35.7)	44 (83.3)	79 (46.3)
New species	1	3	3	20	27
New range records	1	2	9	3	15
Survey effort pre-2005 (Burgess *et al.*, 2007)	0.18	0.20	0.17	0.17	0.18
Survey effort post-2005 (this study)	0.22	0.23	0.19	0.19	0.21
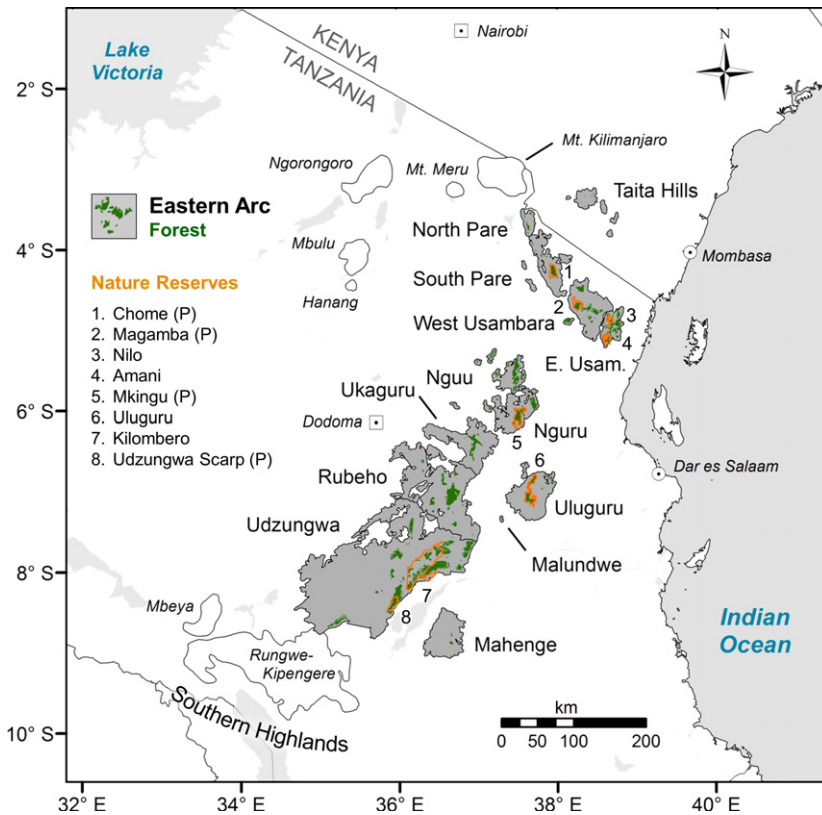
Figure 1 Map of the forested mountains from southern Kenya through Tanzania, adapted from Platts *et al.* (2011). In grey shade are the Eastern Arc Mountains (remaining closed forest in green), with mountain limits that follow Platts *et al.* (2011). North Pare, Nguu, Nguru, Ukaguru, Rubeho and Mahenge mountains were completely or partly unsurveyed for forest vertebrates prior to this study. The network of Nature Reserves ('P' indicates proposed ones) is also shown.

originated from pre-Cambrian basement rocks that were repeatedly uplifted and eroded, with the last uplift occurring since the Pliocene, 7 myr BP (Schlüter, 1997; Stankiewicz & de Wit, 2006). Due to the climatic influence of the Indian Ocean, the EAM have had a relatively stable climate (Mumbi *et al.*, 2008) that favoured the persistence of moist forest on the mountain slopes, but with strong local variation relating to topography (Fjeldså *et al.*, 2010, 2012). The EAM forests are currently isolated from each other by the drier lowland vegetation. The area has been long recognized a distinct biogeographical unit, especially for plants (Lovett & Wasser, 1993), even though the southern limits of the EAM are poorly defined (e.g. Menegon *et al.*, 2011). The most recent estimate of remaining forest cover is 4346 km^2 (Platts *et al.*, 2011), which is less than 30% of the original forest cover (Hall *et al.*, 2009).

Biodiversity data

Despite the known high biological importance and global conservation status, and the wealth of studies conducted, several mountain blocks in the EAM had been hardly surveyed by the early Noughties. As a consequence, the most updated review of biodiversity importance for the EAM was based on limited, or even absent, vertebrate data for Mahenge, Nguru, Nguu, North Pare, Rubeho and Ukaguru mountains (Burgess *et al.*, 2007; but see Doggart *et al.*, 2006).

Since 2005, new vertebrate surveys have been conducted to fill knowledge gaps in nine mountain blocks; the results have

either been published in the primary scientific literature (e.g. Menegon *et al.*, 2008; Rovero *et al.*, 2008), as reports available on specialist websites (http://www.tfcg.org; http://www.easternarc.or.tz), or remain as unpublished material housed within taxonomic experts' databases. Most new surveys were funded during 2005-2009 through the support of the Critical Ecosystem Partnership Fund (CEPF; http://www.cepf.net), which targeted surveys to lesser known mountain blocks within the Tanzanian EAM: North Pare, South Pare, Nguu (also called North Ngurus), Nguru (also called South Ngurus), Rubeho, Ukaguru, Mahenge, Malundwe and southern Udzungwa (Mufindi forests) (for survey details and downloadable reports see Table S1 in Supporting Information).

The new surveys involved experts in each vertebrate class (except fish) and adopted standard inventory methods used in these forests for a number of years (see Doggart, 2006 for methodological details and Table S1 for site-specific details of sampling procedures in recent surveys). In summary, surveys used transect walks and camera-trapping for diurnal primates and medium-to-large terrestrial mammals; nocturnal transect walks and recording of vocalizations for nocturnal primates; bucket pitfall traps with drift fencing, and Sherman's traps, for small mammals; opportunistic searches, bucket pitfall traps with drift fencing and recording of vocalizations for amphibians and reptiles; and observations and mist netting for birds. Indigenous knowledge was also collated using semi-structured interviews. Sampling design and effort varied across forest sites and blocks with greater effort – in terms of area covered and number of sampling

techniques used – allocated to blocks that were previously non- or little surveyed for the majority of vertebrate groups, namely Malundwe, Mahenge, Nguru, Nguu, North Pare and Rubeho (Table S1). In these blocks, the typical survey involved multiexpert teams assisted by local staff each deploying the techniques listed above and hence sampling all groups of vertebrates at each forest site. Expert taxonomists confirmed uncertain species records (see Acknowledgements). Additional data on birds came from Fjeldså et al. (2010, 2012), and J. F. and the late J. Kiure (unpublished data). We compiled all new data on species occurrence from these surveys since 2005, by mountain block, and merged them with the baseline data set (Burgess et al., 2007).

Predictors

We compiled seven non-species data sets as candidate predictors in models aiming to explain species diversity patterns (see below for modelling approach). Data sets were: (1) average annual rainfall, based on analysis of 1997–2006 data from the Tropical Radar Measuring Mission (TRMM; Mulligan, 2006) as derived by Platts et al. (2010); (2) forest area (Platts et al., 2011), log-transformed to linearize the relationship with species richness; (3) forest elevational range (Platts et al., 2011), which correlates with minimum altitude of forest (Pearson's $r = -0.703$, $P < 0.01$) and maximum altitude of forest ($r = 0.853$, $P < 0.001$); (4) estimated forest loss during 1955–2000 (Hall et al., 2009); and (5) human disturbance, derived from disturbance data collected along approximately 500 km of 10-m-wide transects that recorded cutting of trees and poles, and compiled by Ahrends et al. (2011b). As the variables related to disturbance were highly correlated (r min = 0.708, r max = 0.966; P min = 0.015, P max < 0.001), we selected only the percentage of trees cut (trees are stems ≥ 15 cm diameter at breast height with ≥ 3 m straight stem length); (6) mean human population density around each block (Platts et al., 2011); (7) cumulative survey effort per mountain block and taxonomic group. We measured survey effort through a composite index that takes into account (1) the area of the single forests (A) within the mountain block where surveys were conducted and (2) sampling intensity (SI). We scored intensity using a 0–1 scale as follows: 0 = no known studies in that block; 0.2 = limited and non-systematic survey over few localities in the block; 0.5 = systematic survey over many localities in the block; and 1 = extremely thorough and systematic survey covering all forests in the block. The scores were assigned using the baseline information from Burgess et al. (2007) and all newer sources listed in Table S1. Scores are reported in Table S2. We then calculated the cumulative survey effort as

$$\sum_{0}^{i} (A_i \cdot SI_i) / \sum_{0}^{i} A_i$$

where i indicates the forests occurring in the mountain block. The final index is reported in Table S3; (8) funding

for zoological surveys, as a second proxy of overall research effort. Funding data were derived from a database developed by Ahrends et al. (2011b) for all biodiversity inventory and conservation projects that have been taken place in the EAM since 1980 ($n = 134$), when conservation and research interest in the area emerged. Data span approximately three decades (1980–2008). All funding data have been converted to US\$ using the conversion rate at the start year of the project, and have been corrected for inflation by calculating their relative US\$ value in the year 2010 using a GDP deflator (http://www.measuringworth.com). Funding was log-transformed to improve linearity.

Explanatory analysis of biodiversity patterns and priorities

We only considered species that are endemic (E) or regionally endemic (RE) to the EAM, with RE being species that occur in the EAM and adjacent mountains (namely Kilimanjaro, Meru and the Kenya highlands to the north-northwest and the Southern Highlands to the south-west) and/or in the coastal forests from Kenya to Mozambique (Burgess & Clarke, 2000). In addition, within the EAM-endemic species, we identified single-block endemics (SBE) as species that are restricted in their occurrence to a single mountain block. Finally, species were also categorized in terms of extinction risk using the IUCN Red List of Threatened Species version 2014.2 (http://www.iucnredlist.org/). We computed the overall species richness and the numbers of E and SBE species by block to compare the vertebrate importance among mountain blocks. The lack of consistently documented sampling effort across mountain blocks and surveys (which is inherent with a data set that covers a period of more than four decades and across multiple studies) prevented us to estimate species richness (e.g. using rarefaction analysis). However, the addition of new data allows us to update the prioritization of mountain blocks compared to Burgess et al. (2007).

To determine the importance of our seven explanatory variables as predictors of overall species richness (number of species) and number of E and SBE species across sites, we used both hierarchical partitioning analysis (HP) and generalized linear models (GLMs). To determine the independent contribution of each explanatory variable, we used HP with Poisson error distribution (Chevan & Sutherland, 1991). We then fitted each response variable with the explanatory variables using GLM with Poisson error distribution and logarithmic link function (Zuur et al., 2009). In the case of overdispersion, we refitted the models using quasi-Poisson error distribution. To find the minimum adequate model, we used a backward stepwise selection based on the AIC. Both GLM and HP were performed with the software 'R', version 2.15.3 (R Development Core Team, 2013). HP was computed using the package hier.part, version 1.0-4 (Walsh & Mac Nally, 2013).

To investigate the similarity of species assemblages among mountain blocks, and hence assess biogeographical patterns

in species composition, we used the software PAST (http://folk.uio.no/ohammer/past/). Cluster analysis was computed on the Sørensen dissimilarity matrix using the Unweighted Pair-Group Method using Arithmetic average (UPGMA method; Legendre & Legendre, 1998).

RESULTS

Updated vertebrate richness in the EAM

New survey data increased the number of vertebrate species that are block endemic, endemic or regional endemic in the EAM from 170 (Burgess *et al.*, 2007) to 211 (24% increase). The increment is due to 27 species new to science, 15 range extensions for species previously not found in the EAM and one bird species (*Arizelocichla fusciceps*; Shelley, 1893) removed due to taxonomic reclassification (Table 1, Table S4). The new species consist of one mammal, three birds, three reptiles and 20 amphibian species, and range-extended species consist of one mammal, two birds, nine reptiles and three amphibian species (Table 1). Revised vertebrate richness consists of 136 E species (64% of total assemblage, of which 79 are SBE) and 75 RE species (36%). Amphibians and reptiles represent 64% of total assemblage, with 76 and 59 species, respectively (Table 1). For endemics, these two classes contain 75% and 80% of the total E and SBE species, respectively. Among the SBE amphibians, five species are 'hyper-endemic' with a known range restricted to < 10 km² (M. Menegon, unpublished data).

EAM block rankings have changed, particularly for previously unsurveyed sites (Fig. 2). Udzungwa (area = 1765 km²; effort = 0.44) and Uluguru (area = 309 km²; effort = 0.34) remain the top sites for SBE (20 and 13 species, respectively), followed by East Usambara (area = 384 km²; effort = 0.97) with 10 species and Taita (area = 7 km²; effort = 0.50) with eight species. However, Nguru (area = 327 km²; effort = 0.29) and Mahenge (area = 20 km²; effort = 0.25) ranked last in 2007 with no SBE, now contain seven and six SBE species, respectively. West Usambara also holds six SBE species. The remaining blocks have four or fewer SBE species. When considering EAM E species, Udzungwa ranks first with 45 species, followed by Uluguru and East Usambara. Sites that were unsurveyed by 2005 changed their ranking considerably: Nguru, which was low ranked, is now fourth with 35 E species, and Rubeho, Ukaguru and Nguu rank sixth to eighth with 18, 14 and 14 species, respectively. Rankings also differ according to the vertebrate class considered. Nguru mountains, in particular, rank highly for E and SBE reptiles and amphibians (second ranked for E reptiles and amphibians and second ranked for SBE amphibians). With four species of endemic mammals, Rubeho matches Uluguru and East Usambara (Table 2).

In terms of threat status, 145 vertebrate species (69%) have been evaluated against the IUCN Red List criteria, with major gaps remaining in assessments of reptiles and amphibians (56 of the 66 unassessed species belong to these two classes, mainly reptiles). Of the species assessed, 1 is extinct in the wild (the toad *Nectophrynoides asperginis*), 92 are
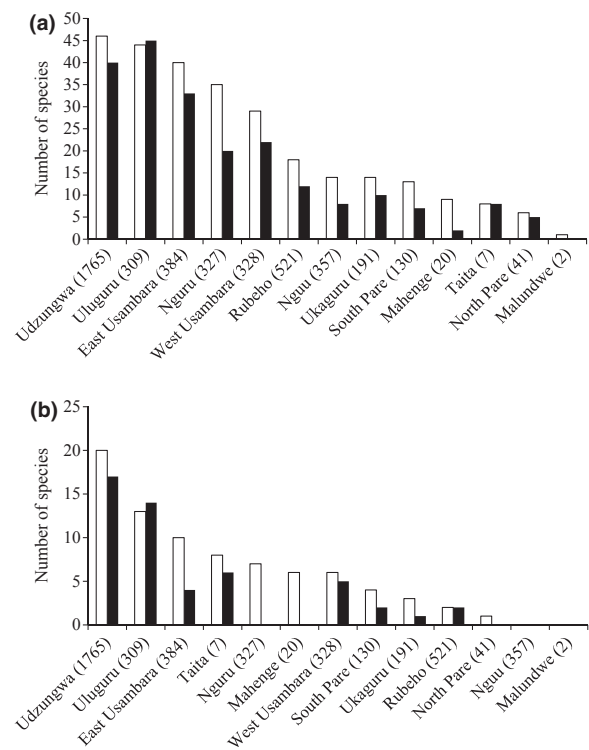
Figure 2 Number of endemic (a) and single-block endemic (b) species in the Eastern Arc Mountains, with blocks ranked by species richness (white bars). Black bars are the baseline values from Burgess *et al.* (2007). In parentheses besides the block name is the closed forest area per block (km²).

threatened with extinction (20 critically endangered, 43 endangered and 29 vulnerable), while of the remaining 52, 11 are data deficient, 38 are least concern and 3 are near threatened. For all classes, the overall incidence of threatened species is 63% in mammals, 44% in birds, 90% in reptiles and 72% in amphibians.

Predictors of species richness

The richness of all forest vertebrates (E + SBE + RE), E only and SBE only, is best explained by forest area, amount of rainfall and funding; combined, these three variables explain 68–73% of variance in species richness between mountain blocks from the hierarchical partitioning analysis (Table 3). This pattern varies when single taxonomic classes are considered (Table 3). For mammals, rainfall has little importance, while forest elevational range is critical (10–21%), along with survey effort (9–20%). This differs only slightly for birds, where, besides forest area and elevational range, forest loss is more important than funding to explain the variance in E species (17%), while for SBE birds, forest elevation is the strongest correlate (41%), followed by rainfall and forest loss. For reptiles and amphibians, rainfall is consistently the top-ranked variable in terms of variance explained (22–47%) followed by forest area and funding, except for SBE reptiles for which funding is slightly more important than rainfall (24%)

and for SBE amphibians for which forest loss (12%) is relatively more important than forest area.

Results for all species categories, including RE only, confirm the general importance of forest extent (= Log forest area + forest elevational range) for mammals and birds relative to its importance for reptiles and amphibians, while rainfall is important for reptiles and amphibians. Funding has similar importance, explaining around 18% of the variance.

Human disturbance (= human density + forest loss + disturbance) explains an average 14% of variance, with the notable exception of RE mammals, E and SBE birds and SBE amphibians for which disturbance accounts for 19–30% of the variance. GLM stepwise modelling supports the results from hierarchical partitioning, as indicated by the significant variables retained by the best models and indicated in Table 3 (see Table S5 for full results).

Table 2 The richness of endemic (E) and single-block endemic (SBE) vertebrates per mountain block and vertebrate class in the Eastern Arc Mountains of Kenya and Tanzania

Mountain block	Birds		Mammals		Reptiles		Amphibians	
	E	SBE	E	SBE	E	SBE	E	SBE
Taita	3	3	0	0	2	2	3	3
North Pare	2	0	0	0	2	0	2	1
South Pare	4	1	1	0	2	0	6	3
West Usambara	8	1	2	0	9	1	10	4
East Usambara	7	0	4	1	14	3	15	6
Nguu	3	0	1	0	3	0	7	0
Nguru	3	0	2	0	15	1	15	6
Uluguru	7	3	4	0	16	4	17	6
Ukaguru	3	0	3	0	3	0	5	3
Rubeho	6	1	4	0	5	0	3	1
Malundwe	0	0	0	0	0	0	1	0
Mahenge	1	0	0	0	3	2	5	4
Udzungwa	8	2	7	4	16	7	15	7
All blocks	23	11	11	5	42	20	60	44

Table 3 The influence of seven predictors of species richness of all forest vertebrates (E+RE), endemic (E) and single-block endemic species (SBE) in the Eastern Arc Mountains of Kenya and Tanzania, quantified by the percentage of variance explained from hierarchical partitioning analysis*

		Log area	Effort	Log funding	Forest elevational range	Human density	Rainfall	Forest loss	Disturbance
All Vertebrates	E+RE	**28.77**†	5.91‡	**19.20**	11.64	1.00	**24.71**‡	5.94§	2.83
	E	**21.97**†	6.45	**14.26**	11.44	3.09	**32.01**†	8.97†	1.82
	SBE	**15.86**	11.70§	**27.44**†	10.82	1.90	**27.38**†	2.28	2.61§
Mammals	E+RE	**32.71**	9.08	**15.08**‡	**20.59**	4.74	8.22	8.17	1.42
	E	**31.90**†	13.83	14.15	**15.71**	3.11	8.04	7.08	6.16
	SBE¶	**30.08**	**19.59**	**19.01**	10.41	7.99	5.67	6.99	0.24
Birds	E+RE	**48.61**†	6.58	**17.03**	**17.57**	1.18	2.83	2.44	3.76
	E	**21.52**	6.77	11.70	**26.24**	9.31	4.11	17.24§	3.10
	SBE	**9.68**	9.27	6.67	**41.28**	5.36	**14.14**	9.18	4.42
Reptiles	E+RE	**17.60**†	6.80	**16.14**	7.25	1.76	**38.57**†	9.45†	2.44
	E	**19.48**†	4.38	**11.85**	8.09	2.27	**40.65**†	9.79†	3.49
	SBE¶	**21.94**	13.52	**23.91**	11.89	3.11	**21.74**†	3.14	0.75
Amphibians	E+RE	**21.77**	3.84	**18.47**	9.91	0.70	**40.44**†	3.76	1.10
	E	**17.12**§	7.41	**12.80**	11.11	1.89	**43.26**†	5.73§	0.67
	SBE	6.38	5.04	**19.56**	3.88	2.20	**46.47**†	12.42§	4.04

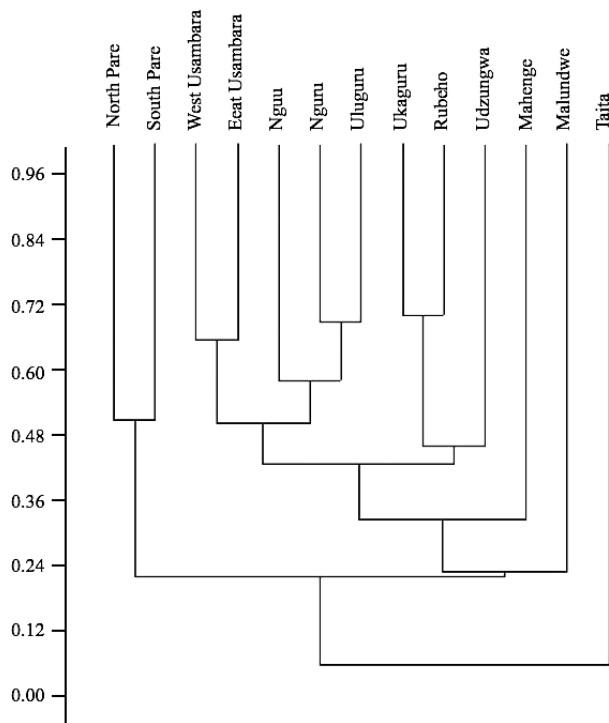*Values in bold are three for each row that contribute the most to the variance.
†Variable significant at $P < 0.001$ from GLMs.
‡Variable significant at $P < 0.01$ from GLMs.
§Variable significant at $P < 0.05$ from GLMs.
¶The model does not fit for excess of zeros. See Table S5 for full details of GLMs.

Figure 3 Dendrogram based on a matrix of the occurrence of endemic and regional endemic Eastern Arc Mountains forest vertebrate species by mountain block, using the Sørensen dissimilarity index.

Patterns in species assemblages

Statistical clustering of mountain blocks by species composition reflects geographical proximity (Fig. 3). Three main clusters are identified: (1) Taita alone, (2) north-western sector (North Pare and South Pare) and (3) 'core' EAM. The latter can be divided into three subclusters: Malundwe and Mahenge (the most dissimilar blocks), central-south EAM (Udzungwa, Ukaguru, Rubeho) and central-north EAM (West and East Usambara, Nguu, Nguru and Uluguru).

DISCUSSION

The importance of targeted surveys

Our study confirms the importance of strategically directing funds and survey effort towards lesser known areas and shows that even the well-known EAM hotspot was understudied. The new surveys further increase the exceptional importance of the EAM in terms of endemic vertebrate species, which for endemic reptiles and amphibians is unmatched in Africa (Tolley *et al.*, 2013; K. Tolley & M.M., unpublished data), while for birds and mammals is paralleled only in the Albertine Rift and Cameroon highlands (Bergl *et al.*, 2007; Plumptre *et al.*, 2007; Fjeldså & Bowie, 2008). For reptiles and amphibians in particular, our new surveys have dramatically improved the previously fragmented

knowledge (see also Loader *et al.*, 2011; Menegon *et al.*, 2011). The findings are also of critical relevance to a planned update and resubmission of a nomination dossier covering selected sites within the EAM as a serial site under the UNESCO's World Heritage Convention.

While we could not estimate total species richness, our analysis allows us to assess predictors of richness with consideration of possible bias from variable sampling effort and funding. Funding explains a consistent portion of variance (details discussed below) while survey effort, which generally explains < 10% of variance in species richness, was relatively more important for SBE (in particular all vertebrates, mammals only and reptiles only), matching the greater sampling effort needed to detect narrow-range species. This implies that additional surveys may discover even more new species and range records in the EAM.

With these considerations in mind, as new surveys targeted previously unsurveyed blocks, it is not surprising these areas have risen in the ranking of EAM blocks. Yet, the changes are dramatic. For example, Mahenge and Nguru have changed from being considered as lacking any SBE to ranking fifth and sixth for SBE, holding eight and six SBE species, respectively. The new data also smooth differences in numbers of EAM endemics between the top-ranked Udzungwa, Uluguru, East Usambara and the least ranked blocks. Nguru and West Usambara have over 20 EAM endemics, and other blocks hold from 5 to 15 EAM endemics.

Predictors of species richness and geographical patterns of composition

The analysis of environmental correlates of species richness confirms the importance of forest area, as previously shown by Burgess *et al.* (2007) for the EAM, and in a number of studies from other tropical areas (e.g. Gascon *et al.*, 1999; Laurance *et al.*, 2002). Interestingly, however, area itself is not always of primary importance, as forest elevational range can be more important, especially for mammals and birds that are more mobile. In the Udzungwa, for example, the existence of forests that are large and have a wide elevational range may explain why relatively large endemic mammals are only found in this block. Forest elevational range explains about five times more variance than forest area alone in SBE birds, perhaps reflecting the fact that a number of EAM birds migrate seasonally along altitudinal gradients (Burgess *et al.*, 2000). Similar considerations apply to SBE amphibians, where forest loss significantly influences species richness. Given that a number of these SBE amphibians are known to be hyper-endemic, sometimes confined to a single valley, further forest loss could remove their only localities.

Rainfall also emerged as an important driver of observed species richness. Its primary influence, especially for SBE and E amphibians, and for E reptiles, has critical conservation implications because it indicates the particularly strong association of these species with the persistence of moist forest. There is growing evidence that the Indian Ocean-driven local

climatic conditions in the EAM have been stable during periods of past global climatic changes (Fjeldså & Lovett, 1997; Mumbi *et al.*, 2008; Finch *et al.*, 2009), and such stability would have been a critical factor driving the remarkable levels of endemism we observe, through either of the non-alternative theories of long-term stability (Fjeldså & Lovett, 1997; Tolley *et al.*, 2011; Loader *et al.*, 2014) and Plio-Pleistocene refugia (Hamilton, 1982). Hence, the protection of small pockets of moist forests on mountain slopes will likely determine the long-term viability of many narrow-range species (Stanley *et al.*, 2005; Lawson *et al.*, 2013).

Funding of biodiversity surveys emerges as a factor of moderate importance (19% of variance for all species), when compared to a similar study on plants where it explained 65% of variance in EAM plant species richness (Ahrends *et al.*, 2011b). Still, there are parallel indications in our study that funding of surveys may bias the perceived richness of vertebrates through a mechanism of circularity that will overlook areas that received little funding initially. That this pattern does not emerge in vertebrates so predominantly as in plants may reflect the fact that surveys have specifically targeted areas that had received little funding previously, hence rebalancing the allocation of resources. Nevertheless, we corroborate the conclusion by Ahrends *et al.* (2011b) that funding for biodiversity surveys, and associated sampling intensity, needs to be considered in the development of models that are attempting to predict species richness using available sampled data.

Human density around forests and human disturbance in the form of trees and poles cutting were found to be poor predictors of species richness. This is perhaps surprising, but there may be a number of explanations. First, the reserved forests across the EAM have been fairly successful at maintaining forest cover (Hall *et al.*, 2009), and therefore, the levels of degradation recorded may be within tolerance for most species. Second, because the field assessment of disturbance is time-consuming, the sample of disturbance transects conducted (approximately 500 km of transect length within over 4500 km^2 of forest in the EAM) may have not fully captured the forest degradation process. Third, these two variables may not adequately describe the multifaceted human disturbance process, for example, because they do not account for hunting (Rovero *et al.*, 2012), or for the possible time-lag between disturbance and species loss (e.g. Brooks *et al.*, 1999; Metzger *et al.*, 2009). However, human density has increased around the EAM, in line with the national trend (National Bureau of Statistics, 2013), which is mainly due to suitable farming opportunities in these mountains, and all people living in the mountains rely on biomass for cooking fuel.

The clustering of mountain blocks by species assemblages corroborates an earlier study showing the non-random, nested pattern in forest birds' composition across the EAM (Cordeiro, 1998), with the assemblages of smallest and/or more peripheral blocks such as Taita Hills, North and South Pare being subsets of those in the largest, 'core' EAM blocks.

Results are even closer to those from an earlier clustering analysis that considered reptiles and amphibians only (Menegon *et al.*, 2011). Geographical proximity is the key explanation for the similarities, probably reflecting the ability of species to persist across forests that were presumably connected by lowland forests in wetter climate periods (Fjeldså & Lovett, 1997; Fjeldså & Bowie, 2008; Menegon *et al.*, 2011). This may have especially applied to Nguu, Nguru and Uluguru that form a tight cluster. All three ranges are oriented parallel to the Indian Ocean and have no significant barriers in between other than dry savanna. Species that were able to disperse at low elevation, especially birds and mammals, would easily persist at all three sites as also indicated by the fact that at the foothills of these blocks remnants of lowland forest persist (e.g. Kanga forest in Nguru).

Conservation of forest vertebrates in the EAM

The great majority of EAM forest is under different forms of legal protection, with the majority falling within the category of 'National Forest Reserve' managed for water catchment, soil erosion prevention and biodiversity conservation. Legally, no exploitation is allowed in these reserves. Forest extent is highly correlated with the extent of protected areas (Spearman's $r = 0.99$, $P < 0.0001$, data in Platts *et al.*, 2011), indicating that a comprehensive network of protected areas is the single, most important approach to sustaining the current richness of vertebrates in the EAM.

Forest reserves in Tanzania mirror the global trend of biodiversity impoverishment within tropical forest protected areas (Laurance *et al.*, 2012) as they are generally not adequately protected (e.g. Rovero *et al.*, 2012). The reasons for poor protection largely relate to the chronic lack of resources and capacity within the Tanzania Forest Service (TFS). To enhance management effectiveness, through TFS some of the forest reserves in the EAM have been upgraded to forest Nature Reserves, with the selection of sites for upgrading largely based on new knowledge from our surveys (e.g. Menegon *et al.*, 2008). The current network of Nature Reserves and proposed Nature Reserves is shown in Fig. 1. While these sites cover the majority of forests of highest biodiversity importance in line with our results, they still omit key sites in the Mahenge and important sites in the Ukaguru and Rubeho, which are among those unsurveyed before our study. In addition to confirming the justification of these upgrades in legal status for existing reserves, the surveys reported here show the high value of formerly neglected or even unidentified forests such as Ilole in the Rubeho. This small forest had not been surveyed by biologists before 2007 when surveys recorded the presence of several EAM E species (Rovero *et al.*, 2008), which in turn prompted conservation initiatives that have resulted in this forest being protected as a village land forest reserve.

While the network of formally protected forests in the EAM is an asset, the long-term capacity to protect the forests needs enhancing to be effective. Hence, besides the continued

input of foreign donors, novel mechanisms of income generation will need to be explored by the Government of Tanzania, such as water PES schemes (e.g. Lopa *et al.*, 2012), pilot REDD+ schemes (http://www.tfcg.org) and boosting tourism to the area. Although the value of nature-based tourism to the EAM is lower than that generated by Tanzania's savanna large reserves, the potential revenues from this sector are considerable and enhance the case for sustainable forest management (Bayliss *et al.*, 2013). Sustained forest protection needs to be coupled with improved environmental awareness and sound involvement of adjacent communities towards novel approaches to forest management. Tanzania has an excellent track record in decentralization of natural resource management through the well-framed Participatory Forest Management (PFM) framework, which has been shown to deliver environmental protection in woodland and forest areas (Blomley *et al.*, 2008; Persha & Blomley, 2009; Nielsen, 2011). However, in EAM the benefits to surrounding communities from the PFM regime are much lower than in dry miombo woodlands, because the high human density and the global biodiversity and national water supply importance of the mountains motivate strong and centralized law enforcement by TFS, which cannot be compatible with intense village-level utilization of the forests. Hence, the alternatives of on-farm income generation schemes, PES, tourism and other development activities are preferred to compensate communities for the loss of access to forest resources.

The Nature Reserves, proposed Nature Reserves and Udzungwa Mountains National Park have been proposed as the EAM serial natural World Heritage Site (WHS). The Government of Tanzania prepared and submitted the full dossier for this site in 2010 (United Republic of Tanzania, 2011), but due to misunderstandings within the Tanzanian Government, the application was withdrawn. Our results further strengthen the knowledge of the 'Outstanding Universal Value' of the EAM. In particular, the comparison of richness of E and RE vertebrates in the EAM versus six tropical forest sites that are already WHS, and for which comparable data on endemic vertebrates are available (United Republic of Tanzania, 2011), shows that the EAM rank among the top sites, and for amphibians and reptiles the EAM is *the* top site for endemism. Similarly, relative to other species-rich tropical African mountain forests such as the Albertine Rift and Cameroon Highlands, the number of endemic mammals and birds is comparable, while for amphibians and reptiles the EAM becomes the top site. This result is mirrored in the recent gap analysis of biodiversity sites that qualify for WHS nomination, as five of 46 'most irreplaceable sites' globally, which are not included in the existing network of biodiversity WHS, are within the EAM (Bertzky *et al.*, 2013; Le Saout *et al.*, 2013).

We conclude that strategically placed surveys are extremely important as even well-known and recognized hotspots can remain severely understudied, with significant consequences for conservation planning. Our study confirms and further increases the known biological values of the EAM and shows that these values are mainly related to area, altitudinal range and moisture of forest habitats. The natural forests have declined over many decades and are now largely confined to various types of reserves. The most valuable of these reserves are being upgraded to National Park and Nature Reserve status, and there are efforts underway to recognize the most important sites under the 'Outstanding Universal Value' criteria of the World Heritage Convention. Our study confirms the EAM as a clear gap in the global network of WHS and supports efforts to update and resubmit the nomination dossier for the EAM.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Reference sources for sampling methods and results of forest vertebrate surveys.

Table S2 Survey effort scores by EAM forest and block.

Table S3 Index of survey effort by EAM block.

Table S4 List of vertebrates by mountain block.

Table S5 Results of GLM models for predictors of richness of forest vertebrates.

BIOSKETCH

Francesco Rovero is a tropical conservation scientist with research interests in biodiversity monitoring, ecological modelling of forest mammals and protected area management. He is the Curator for Tropical Biodiversity at MUSE – Museo delle Scienze (http://www.muse.it/en). This research group has worked on the biogeography, ecology, taxonomy and conservation of forest vertebrates in East Africa, and especially Tanzania, for over 10 years. Coauthors have all been engaged collaboratively in forest vertebrate surveys and ensuing taxonomic and biogeographical assessments in the Eastern Arc Mountains in the framework of the Critical Ecosystem Partnership Fund (http://www.cepf.net).

Author contributions: F.R. and N.D.B. conceived the ideas; F.R., M.M., J.F., L.C., N.D., C.L., G.N., N.O., A.P. and A.A. collected the data; F.R., M.M., D.S. and A.A. analysed the data; and all authors contributed to the writing, which was led by F.R. and N.D.B.

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