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Delimiting tropical mountain ecoregions for conservation

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SUMMARY

Ecological regions aggregate habitats with similar biophysical characteristics within well-defined boundaries, providing spatially consistent platforms for monitoring, managing and forecasting the health of interrelated ecosystems. A major obstacle to the implementation of this approach is imprecise and inconsistent boundary placement. For globally important mountain regions such as the Eastern Arc (Tanzania and Kenya), where qualitative definitions of biophysical affinity are well established, rule-based methods for landform classification provide a straightforward solution to ambiguities in region extent. The method presented in this paper encompasses the majority of both contemporary and estimated preclearance forest cover within strict topographical limits. Many of the species here tentatively considered 'near-endemic' could be reclassified as strictly endemic according to the derived boundaries. LandScan and census data show population density inside the ecoregion to be higher than in rural lowlands, and lowland settlement to be most probable within 30 km. This definition should help to align landscape scale conservation strategies in the Eastern Arc and promote new research in areas of predicted, but as yet undocumented, biological importance. Similar methods could work well in other regions where mountain extent is poorly resolved. Spatial data accompany the online version of this article.

Keywords: boundary placement, conservation priority, Eastern Arc Mountains, ecological regions, ecosystem services, mapping, plant endemism, population pressure, topography

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INTRODUCTION

Ecological regions (ecoregions) are widely employed as units for conservation priority setting (Olson & Dinerstein 2002; Burgess *et al.* 2006). By aggregating ecosystems with similar biophysical characteristics, interdependences and spheres of influence within ecoregions, assessment and management can target the system as a whole and avoid any disconnect between science and policy. This holistic approach is more faithful to environment–ecosystem interconnections, including the role of human populations, but by definition imposes strict and static divisions on complex and ever changing landscapes. Careful delineation is therefore crucial. Landform, geology, climate, vegetation and evolutionary history, as well as cultural and political considerations, are all important (McMahon *et al.* 2004). In practice, different criteria favour different objectives and no single solution is optimal for all applications in all regions (Olson *et al.* 2001).

Some biogeographical units such as mountains, wetlands and islands appear by their nature to be clearly defined in space. In the case of mountains, however, there is no universally accepted method for marking the transition to lowlands, and thus no consistent way of defining precisely the geographical limits of a mountainous region (Gerrard 1990). The essence of the problem, as in any ecoregion, is that environmental gradients are continuous (from sea level to mountain top) and so any spatial dichotomy is necessarily subjective. Freely available digital elevation data, together with improvements in desktop mapping software, have brought advances in the development of a systematic process by which to define and study mountains. Practitioners can now experiment with different ways of bounding their region of interest, so that qualitative definitions of biological affinity may where appropriate progress to spatially explicit rule-based algorithms, increasing the prominence of such regions and their specific management challenges on the political stage (Browne *et al.* 2004; McMahon *et al.* 2004).

As assessment mechanisms for biodiversity and ecosystem services move towards implementation within international frameworks (Larigauderie & Mooney 2010), there is a requirement for rule-based definitions that can resolve
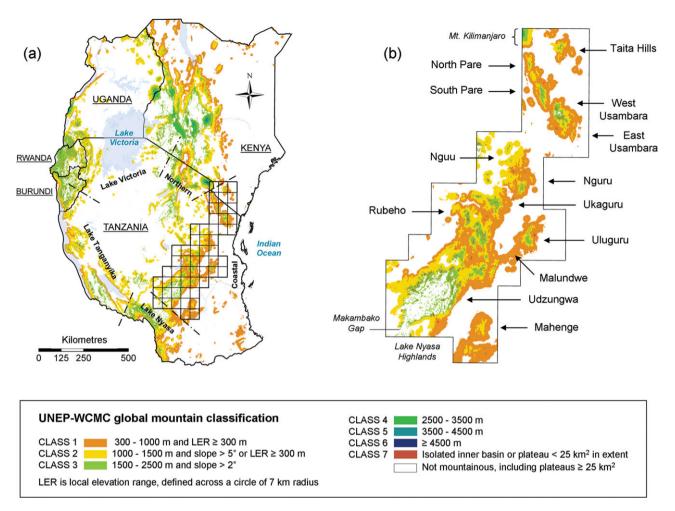
Figure 1 Global mountain typology defined by UNEP-WCMC at 1 km resolution. (*a*) East Africa, showing divisions in Tanzanian forest on the basis of geology and climate (from Lovett 1990): Coastal, Eastern Arc and Northern forests are all under the direct climatic influence of the Indian Ocean (rather than the Great Lakes), but only the Eastern Arc is on igneous and metamorphic rock. (*b*) Zoomed perspective of the 13 Eastern Arc ranges (blocs).

ambiguities in the placement of ecoregion boundaries. In the present study, using the Eastern Arc of Tanzania and Kenya as an example, we discuss some of the challenges and uncertainties in defining tropical mountain ecoregions. This chain of 13 block-faulted massifs harbours one of the world's most important concentrations of biodiversity across a series of fragile sites (Brooks *et al.* 2002; Mittermeier *et al.* 2004). The 'Eastern Arc Mountains [sic] Forests' have recently been proposed for UNESCO World Heritage status (http://whc.unesco.org/), and will soon be subject to increased international attention as the United Nations REDD Programme (Reducing Emission from Deforestation and Forest Degradation in Developing Countries) is piloted in Tanzania (Burgess *et al.* 2010). We propose for the first time a rigorous set of topographical limits for these mountain habitats, using as a starting point the global mountain topology developed by the UNEP World Conservation Monitoring Centre (UNEP-WCMC; Kapos *et al.* 2000). Increasing the spatial resolution from 1 km to 90 m, we rescale terrain

parameters using empirical and remotely sensed data on the distribution of endemic plant species and mountain forests respectively, before bounding the ecoregion according to topographic prominence and established biogeographical distributions.

A qualitative definition for the Eastern Arc

The Eastern Arc Mountains were first described as distinct from surrounding Afromontane habitats in the 1980s due to the exceptional proportion of rare species (Lovett 1985). The distinction is qualitatively explained according to key environmental characteristics thought to underlie the high levels of endemism (Fig 1*a*): first, the great age of the Precambrian crystalline and metamorphic substrate compared to geologically more recent volcanoes such as Kilimanjaro and Meru (>30 million versus <2 million years old; Schlüter 1997); and second, the relative consistency of rain-bearing winds from the Indian Ocean compared to more

variable climatic regimes within the great lake catchments of Nyasa/Malawi, Tanganyika and Victoria. Accordingly, the chain extends roughly 750 km from the Taita Hills in south-east Kenya to the Udzungwa Mountains in south-central Tanzania; volcanoes to the north are excluded (different substrate), as are highlands south of the Makambako Gap (geologically younger and rainfall patterns not directly influenced by the Indian Ocean).

We identified the 13 most commonly-cited ranges (blocs; Fig. 1*b*). Sometimes omitted are: the Taita Hills (the only bloc north of the Kenya-Tanzania border; see for example Burgess *et al.* 2009); the Nguu (sometimes combined with Nguru; see Newmark 2002); and Malundwe Mountain, owing to its small extent and position within a chain of low elevation hills (see Stanley & Olson 2005). An occasional addition is Image, but this mountain is more usually included in Udzungwa (Mbilinyi *et al.* 2006).

Mountain limits

The lack of a systematic basis for boundary placement in the Eastern Arc has meant that the precise spatial extents depicted have varied from study to study, hindering information exchange and multilateral action in response to new data or changes on the ground. Mountain limits have been defined variously by hand, using elevational contours, forest or reserve boundaries, or a combination of these factors (for example see Olson *et al.* 2001; Doggart *et al.* 2006). Many depictions can be traced back to Lovett (1992): drawn from contours on a Shell Road Map, these boundaries were intended as diagrammatic and heuristic; however a number of derivatives are now in common usage, conspicuous in their repetition of shortfalls in the original. A 1000 m cut-off for the Taita Hills, for instance, depicts bloc-extent far to the west of the mountains proper, but excludes important sites for conservation in the east.

Elevation offers a simple, intuitive, but often insufficient method for delimiting mountain regions (Messerli & Ives 1997). With respect to plant endemism in the Eastern Arc, one convention is to impose a uniform lower limit of 500 m (see for example government reports and the World Heritage application), intended to distinguish montane habitats from the nearby coastal forests (Lovett *et al.* 2000). We find this definition to be too strict in the east, excluding patches of forest from the lower slopes of six mountain blocs (Platts *et al.* 2010). Conversely, because the East African interior is characterized by a highland plateau, almost all non-mountainous land on the western side exceeds elevations of 500 m. Similarly for herpetofauna, species turnover is highest at elevations of *c.* 400 m in the north-east, but *c.* 800 m in the south (Poynton *et al.* 2007).

A global mountain typology

Effective mountain delineation across all aspects requires consideration of not just elevation, but also steepness of slope and terrain roughness (Gerrard 1990). Implementing these criteria on a global scale, UNEP-WCMC developed a map of the world's mountains and mountain forests by classifying 1 km^2 land parcels according to elevation, slope and local relief (Kapos *et al.* 2000; Blyth *et al.* 2002). The classification consists of six elevational bands, with terrain constraints strictest at low elevations (Fig. 1). Whilst this typology effectively represents the Eastern Arc on a world map, it is too broadly defined to identify all features important at the site level or to distinguish between adjacent ranges (for example South Pare versus West Usambara; Fig. 1*b*). Kapos *et al.* (2000) suggested that for quantitative applications at sub-national scales their map could be verified and potentially refined using higher-resolution vegetation data, together with an appropriate measure of relative relief; we test these criteria in the context of the Eastern Arc Mountains.

MATERIALS AND METHODS

Regional refinements to the global typology

Elevational zonation
We adhered mainly to globally defined elevational classes (Fig. 1), with the exception of the lowest mountain category, which was applied without the 300 m lower limit. As in other regions where mountains occur along a coastline (see for example Nordregio 2004), marked topography and associated forest vegetation extend almost to sea level. For higher elevations, the hypsographic curve for eastern Tanzania and south-east Kenya (cumulative height versus relative area) exhibits similarities with the breakpoints defined by UNEP-WCMC: frequencies are highest for land at elevations of 1000–1500 m, with a further change in trend at elevations *c.* 2500 m. The unqualified inclusion of all land above 2500 m elevation is perhaps inappropriate for regions with large highland plateaus (see Meybeck *et al.* 2001), but is of little consequence here where only mountain summits exceed this elevation.

Terrain parameters
The spatial resolution of the entire typology was increased from 1 km to 90 m. Shuttle Radar Topography Mission elevation data (Jarvis *et al.* 2008) were extracted for the 56 half-degree grid squares that intersect with the Eastern Arc (Fig. 1) and resampled from a three arc-second geographic projection to a 90 m equal-area conic projection (Africa Albers). Slope constraints were increased from 5° to 10° (class 2) and from 2° to 5° (class 3) to correct for the greater topographic heterogeneity captured per unit area at this finer resolution.

At the global scale, the local elevation range parameter (hereafter, LER$_{RADIUS}$) is intended to capture 'older mountains of regional significance' (Kapos *et al.* 2000). Eastern Arc blocs consist entirely of such old weathered slopes, but in some cases are relatively small and, particularly in the east, rise abruptly from surrounding plains. A parameterization of the LER better suited to regional-scale analysis was therefore sought. With a view to maximizing the inclusion of forest habitats and endemic plant records within a minimal

mountain area, we tested LER radii in the range 250 m to 2 km and thresholds in the range 5% to 30% (of the radius). In exploratory analyses, larger radii led to excessive buffering around the base of the mountains or, with stricter thresholds, the omittance of outlying peaks; smaller radii returned patterns akin to the slope parameter, which is roughly equivalent to LER_{90m}.

The final step in the derivation of each variant of this regional typology was to apply a spatial filter, such that grid squares adopted the majority mountain class within a 500 m radius. This resolved fine-scale anomalies in raster grids, aiding the transition to vector format.

Matching to mountain vegetation
The decision of which parameterization was best suited to the Eastern Arc was guided by overlaying high-resolution (1 ha) vegetation data. Indigenous broadleaved forests in the Taita bloc were identified from SPOT multi-spectral satellite images (Clark & Pellikka 2009). Tanzanian forests were based on data acquired from the Tanzanian Ministry of Natural Resources and Tourism (MNRT 1997; updated with later imagery from 2000 onwards by the Remote Sensing and GIS Laboratory, Sokoine University of Agriculture, Tanzania). We extracted all forest classified as submontane, montane or upper-montane, and additionally considered any lowland forest contiguous with a submontane patch, thus removing the elevational bias of vegetation classification (see Pócs 1976; Lovett & Pócs 1993; Hall *et al.* 2009). These estimates were then corrected according to Mbilinyi *et al.* (2006), Conservation International (2008), Marshall *et al.* (2010) and local knowledge (see for example http://celp.org.uk/projects/tzforeco/). In total, we identified a forest area of 4388 km^2.

Given that *c.* 70% of forest cover has been lost since the beginning of the 20th century (S. Willcock, unpublished data 2010) and that forests on some eastern aspects might regenerate further downslope if it were not for land-use barriers and frequent burning, it was appropriate to also consider estimates of 'palaeoecological' extent (Hall *et al.* 2009; Tanzania only). Hereafter, these estimates are termed 'preclearance' rather than palaeoecological. Forest would have extended beyond the base of the mountains during interglacial periods (for example Holocene and Eemian) and consisted of different vegetation assemblages in cooler, potentially drier environments of lower CO_2 concentration associated with the last glacial period (*c.* 10 000–114 000 yrs BP; Elenga *et al.* 2000; Vincens *et al.* 2007).

Lastly, we overlaid point distributions for 378 species of vascular plants strictly endemic to the Eastern Arc (according to a 500 m lower limit). Over 2000 spatially referenced herbarium specimen records were available (http://www.tropicos.org/), representing 77% of all strict-endemics and spanning all plant growth forms. To investigate the efficacy of the 500 m lower limit for endemism, and to avoid bias resulting from such a convention, we further considered the distributions of 53 'near-endemic' plant species

(455 records, some below 500 m), documented only within the half-degree cells (Fig. 1*b*) and whose known distributions do not extend to coastal forests, Neogene Volcanoes or the Lake Nyasa Highlands. Based on locality information supplied with these records, we assumed a spatial accuracy of one arc-minute (<2 km).

Bounding the chosen regional typology

Amalgamating classified features
First, adjacent mountain classes were dissolved such that each spatially distinct feature was represented by a single polygon. With the exception of small isolated fragments (<1 km^2 and >1 km from nearest neighbour), these features were buffered by 1 km and then simplified and smoothed using bend reduction and polynomial approximation tools in ArcGIS Desktop 9.3.1 (exponential kernel, tolerance = 1 km). This method ensured the preservation of all mountainous features on a 1 km grid (a popular format for regional mapping) and yielded topologically simpler boundaries that additionally enclosed unclassified habitats benefiting from close proximity to complex relief. Following Blyth *et al.* (2002), isolated inner basins and plateaus were filled if less than 25 km^2.

Mountain selection based on relative relief
The distinction between a mountain and a hill is largely semantic, with equivalent relative relief considered mountainous in one region whilst merely hilly in another (OED [Oxford English Dictionary] 1989). It was however appropriate to make such a distinction in the Eastern Arc so that minor relief not commonly perceived as mountainous could be systematically removed. Thompson (1964) suggested a topographic prominence of 2000 ft to be a good rule of thumb, which we rounded down to the metric equivalent of 600 m. A cluster of features, bounded as above, was considered 'mountainous' if attaining an altitude of at least 600 m relative to adjacent elevations; 'hilly' clusters (<600 m prominence) were included in the ecoregion only if known to support natural forest vegetation and/or strictly endemic plant species.

RESULTS

Sensitivity to local elevation range

The biggest changes in overall mountain area resulted from varying the LER threshold according to fixed percentages of its defining radius (Table 1). The lowest threshold (5%) was too permissive, merging adjacent range-boundaries and including minor undulations throughout the lowlands (Fig. 2). Higher thresholds were more effective in terms of forest and endemic plant records captured per unit area, but if too high (30%) then lower slopes and mountain foothills were curtailed. A 20% threshold provided the best compromise between forest inclusion and range distinction. With the threshold percentage held constant, changing the LER radius

Table 1 Mountain area and forest sites included as a result of different calibrations of the local elevation range parameter (LER radius/threshold, mountain classes 1–2). Analyses conducted within Eastern Arc half-degree grid squares using 90 m elevation data and slope thresholds of 5° (class 2) and 10° (class 3); otherwise mountain classification follows UNEP-WCMC, but with no lower limit in class 1. *Mountain typology from which Eastern Arc boundaries were derived (Appendix 2, available online at http://www.journals.cambridge.org/enc2011001).

Calibration	Mountain area (10^3 km^2)	Forest (% included)		Plant endemism records (% included)	
		Current	Preclearance	Strict-endemics	Near-endemics
Threshold = 0.05 × LER radius					
LER_{250m}	86	99.8	99.7	99.4	96.3
LER_{500m}	98	99.9	99.8	99.4	96.3
LER_{1km}	95	99.7	99.8	99.5	97.4
LER_{2km}	88	99.8	99.8	99.5	97.4
Threshold = 0.1 × LER radius					
LER_{250m}	55	98.7	98.3	99.1	95.4
LER_{500m}	62	99.2	99.1	99.1	95.4
LER_{1km}	62	98.7	99.1	99.1	95.2
LER_{2km}	61	97.8	98.8	99.3	95.4
Threshold = 0.2 × LER radius					
LER_{250m}	39	91.2	91.6	98.7	92.1
*LER_{500m}	**43**	**93.9**	**94.4**	**98.6**	**93.2**
LER_{1km}	41	92.4	93.4	98.6	91.9
LER_{2km}	37	90.2	91.2	93.8	85.3
Threshold = 0.3 × LER radius					
LER_{250m}	30	83.9	81.7	98.4	91.7
LER_{500m}	33	87.3	86.8	98.4	91.2
LER_{1km}	31	86.0	84.5	98.1	86.6
LER_{2km}	28	82.7	79.7	92.9	82.5
Eastern Arc boundaries	48	99.0	99.3	99.1	95.2
[Including plateaus]	[52]	[99.0]	[99.3]	[99.7]	[96.7]

affected polygon complexity but had little impact on overall mountain area. Small radii tracked closely fine-scale changes in relief; large radii better represented broad-scale trends in the landscape. Both LER_{500m} and LER_{1km} worked well, but we preferred the former because slightly more forest and endemism records were included, and because the latter excluded lower slopes in south-west Mahenge (inspection of three-dimensional elevation).

At this level (LER_{500m}, 20% threshold), 94% of the estimated forest area (both present-day and preclearance) was classified as mountainous. The remaining 6% was largely within 1 km of a classified feature and so would be captured by the ecoregion boundary (Table 1). One exception was open-canopy forest in the lowest parts of Matundu (south-east Udzungwa), which was omitted by even the most permissive LER threshold. Respectively, 99% and 93% of records for strictly and nearly endemic plant species originate from areas classified as mountainous by the chosen typology.
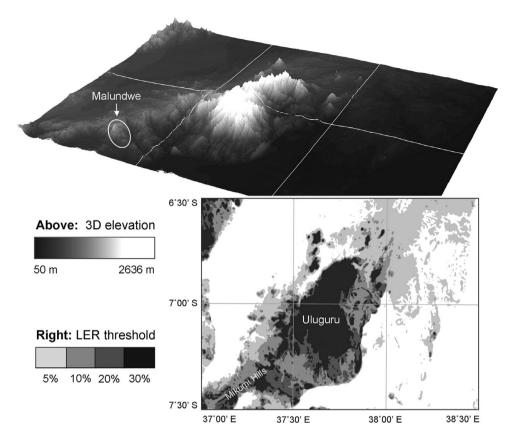
Boundary placement

Polygons corresponding to the south-east slopes of Mt. Kilimanjaro were spatially distinct and so straightforward to remove (Fig. 3). In the south, the Eastern Arc is distinguished from adjacent highlands by climatic influence and vegetation type rather than landform. Consequently, the Udzungwa bloc had to be divided manually from moorlands south-east of the Makambako Gap: we followed the Mpanga River upstream from the Kilombero Valley towards the southern perimeter of Mufindi Scarp Forest Reserve, and then traced this west to dissect the polygon fully.

Within the Eastern Arc chain, the majority of range boundaries were clearly distinguished (Fig. 4). Exceptions occurred for those blocs separated by steep-sided river valleys (Ukaguru versus Rubeho versus Udzungwa), in which cases the divisions were imposed *post hoc* by overlaying the respective river paths (Mkondoa and Great Ruaha Rivers). The most problematic bloc to delineate from surrounding terrain was Malundwe, a 1259 m peak within the Mikumi Hills (Fig. 2). The explicit delineation of this mountain and its small area of forest (<3 km^2) was important for consistency with previous studies, but parameter combinations strict enough to isolate it resulted in the oversimplification or omission of marked topography elsewhere (for example LER_{2km} with 30% threshold). Since the Mikumi Hills in their entirety are rarely considered part of the Eastern Arc chain, we distinguished

Figure 2 Sensitivity of the regional mountain typology to local elevation range (LER, radius = 500 m). Upper pane: elevation in the Uluguru bloc (×5 vertical exaggeration). Lower pane: variations in extent resulting from different LER thresholds (% of radius).

the small Malundwe peak and its forest patch using a 900 m elevation contour, buffered and simplified as for the other blocs (Fig. 4). An alternative delineation that retains the Mikumi relief is provided (Appendix 1, available online at http://www.journals.cambridge.org/enc2011001).
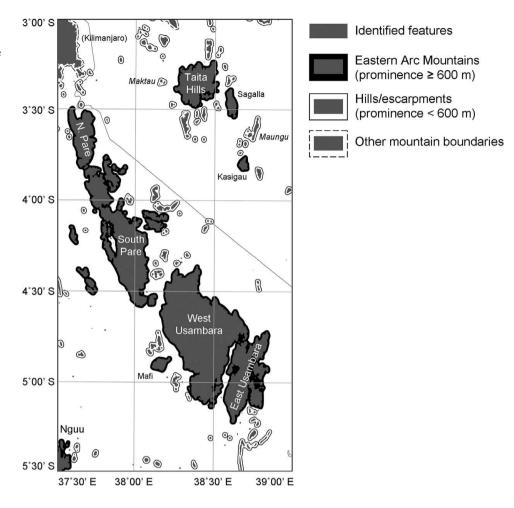
The proposed boundaries enclose a total area of *c*. 48 000 km^2 (52 000 km^2 including plateaus). Elevations range from 121 m to 2636 m above mean sea level, with both extremes corresponding to the highly prominent Uluguru range (Table 2). The 600 m elevation cut-off for relative relief proved appropriate, with only five 'hilly' features warranting inclusion on the basis of forest cover and/or plant endemism: two in Matundu (south-east Udzungwa), one west of the Nguu Range, and two in the Taita Hills. The last support locally endemic plant species: *Encephalartos kisambo* on the Maungu Hills and *Monadenium guentheri* on Maktau Hill, east and west of the main Taita bloc, respectively (Fig. 3). Handeni Hill, 50 km equidistant from West Usambara and Nguu, might have been included on similar grounds, but these forests are more usually associated with coastal vegetation.

The boundaries capture over 99% of all present-day and preclearance forest (Table 2), the lowest parts of Matundu being the only exception (beyond the south-central perimeter of Kilombero Nature Reserve). This area could be included *post hoc* (Appendix 1, available online at http://www.journals.cambridge.org/enc2011001). Non-woody species collected from mid-elevation plateaus in south-west Udzungwa (for example *Oldenlandia oxycoccoides*) might

be considered strict-endemics by elevational criteria, but are not included by either the global or regional mountain typologies (slopes shallower than 2° and 5°, 1 km and 90 m resolutions, respectively). At both scales, steep plateau margins are considered mountainous; thus, depending on the application, Udzungwa plateaus could be included *post hoc* (Fig. 4). Alternatively, dry western margins could be removed, restricting Udzungwa to just those forested slopes benefiting from high orographic rainfall.

Of the 53 near-endemic plant species, at least 30 have been recorded exclusively within the topographical limits defined here (up to 40 if we allow for spatial error in collection localities). Unless additional specimen data suggest otherwise, these species could be revised to strictly endemic. Most other near-endemics have been collected within 10 km of the Eastern Arc boundary, and all within 20 km. Magombera Forest, for example, occupies a lowland position 6 km east of the Udzungwa bloc. Vegetation is predominantly of the kind common in coastal forests, but the presence of some characteristic Eastern Arc flora (for example *Dialium holtzii* and *Isoberlinia scheffleri*) and fauna (for example Udzungwa Red Colobus monkey *Procolobus gordonorum*) suggests past connectivity to higher elevation forests to the west. Such species persist in lowland areas like Magombera owing to their proximity to the coast rather than altitude or slope *per se*; instead of a qualitative definition of near-endemism, the vast majority could be effectively defined as occurring only within the Eastern Arc perimeter and up to 10 km or 20 km beyond.

Figure 3 Boundary placement in the northern blocs. Features identified as 'mountainous' by the chosen typology were aggregated within simplified boundaries and distinguished as mountains or hills/escarpments depending on their prominence relative to adjacent elevations. Italicized hill names indicate inclusion on the basis of plant endemism.

Protected areas

Less than 10% of the Eastern Arc remains forested, compared with 37% preclearance cover. Notwithstanding spatial errors and misclassifications in the protected area and land cover data, we estimated that 75% of present-day forest lies within the protected area network (Table 2, Fig. 4). A further 50 km² corresponds to forest reserves proposed but not yet gazetted, mainly in South Pare, East Usambara and Udzungwa. Other areas are traditionally managed or in private estates, and so are not represented in the database of protected areas used here (UNEP-WCMC 2009). In Kenya, forests are gazetted only within Kasigau Forest Reserve. Forests in the Tanzanian blocs are more widely protected by the state, consisting of both forest reserves (1909 km²) and nature reserves (785 km²) (Nilo and Amani in East Usambara, Kilombero in Udzungwa, and Uluguru). A further 586 km² of Eastern Arc forest lies within three national parks, namely Udzungwa Mountains (north-east Udzungwa), Mikumi (all of Malundwe) and Mkomazi (north-east South Pare).
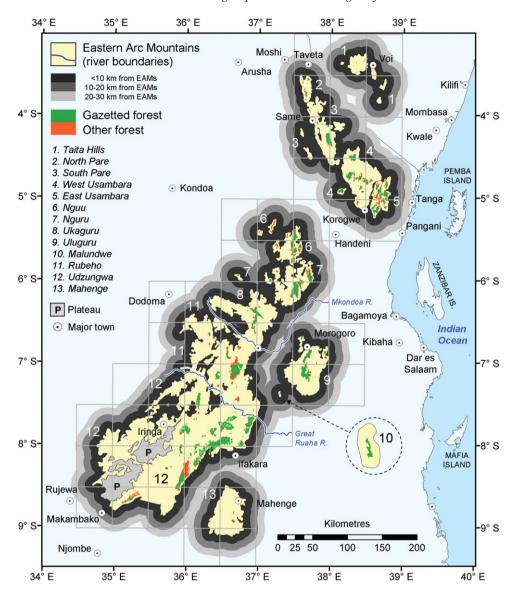
Forest estimates may contain some woodland, up to an eighth of the total, accounting for the lack of protection in some blocs (for example North Pare). The forest area within reserves may also be overestimated due to fragmentation resulting from mixed forest cultivation plots and long-lived fire-maintained grasslands (Finch & Marchant 2011). Conversely, forest regrowth in depopulated areas outside reserves is likely to be underrepresented.

Human populations

At the time of the 2002 Tanzania census, we estimate that the Eastern Arc had a population of *c*. 2.2 million people (2.35 million people if including the Udzungwa plateaus) and that a further 5.4 million people lived within 30 km (Table 2). Mean and median population densities are around 15% and 250% above the national averages for Tanzania, respectively (Fig. 5). Median density (more representative of rural communities than the mean) decreases with increasing distance from the bloc perimeters, up to a distance of 30 km (Figs 4 and 5). Major towns situated within the boundaries include Same (South Pare), Korogwe (West Usambara), Kilosa (Ukaguru), Mpwapwa (Rubeho) and Iringa (Udzungwa), with Morogoro and Ifakara just outside the Uluguru and Udzungwa blocs, respectively. According to these estimates, population densities are highest in West Usambara and North Pare, followed by East Usambara and Uluguru (Table 2).

Figure 4 Ecoregion boundaries, overlaid with forest distributions and protection status. Mid-elevation plateaus in Udzungwa are an option for inclusion (grasslands/heathlands but no natural forest). The majority of 'near-endemic' plant species have been collected within 10 or 20 km of the ecoregion boundary. Density of rural persons is highest within 30 km.

DISCUSSION

Ecoregions are useful tools for making explicit the strong biogeographical affinities that exist within many regions of the world. Where consistently defined, they provide a spatial platform for monitoring, managing and forecasting the health of the constituent ecosystems, as well as the people reliant upon them for natural resources. Communities living in and around tropical mountains benefit from lower ambient temperatures, access to forest products, clean potable water, improved agricultural potential and fewer vectors for disease (for example mosquitoes). Advantages such as these are evident from the decrease in rural population density with increasing distance from the Eastern Arc boundary, a trend also affected by restrictions on human settlement in adjacent game reserves. Large-scale studies suggest a general pattern of human pressures in biologically important regions (Cincotta *et al.* 2000; Balmford *et al.* 2001; but see Joppa *et al.* 2009), driven by real or perceived benefits or by extraction frontiers, such as mining or logging, which open up previously remote
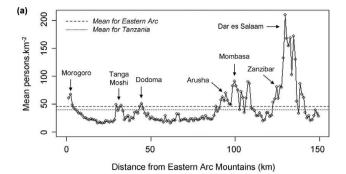
environments for human settlement (Joppa *et al.* 2010; Scholte & de Groot 2010).

In common with much of tropical Africa, the population of Tanzania has increased dramatically over the last half century, from 10 million people in 1960 to 42 million people in 2008 (http://data.worldbank.org/), with growth rates highest in urban areas and mountain foothills. Kenya has experienced a similar population boom, from eight million to 39 million people over the same period. Population growth is exerting increasing pressure on water supplies, energy production and land for agriculture. Demand for timber, poles and charcoal is also increasing as stocks in more accessible Miombo woodlands and coastal forests continue to diminish under pressure from urban centres such as Dar es Salaam (Ahrends *et al.* 2010). Increased resource demand and intensified land use have direct implications for forest health and local livelihoods, as well as more diffuse impacts such as biodiversity loss and the release of sequestered carbon into the atmosphere (Kohler *et al.* 2010).

Table 2 Summary of the Eastern Arc ecoregion, detailed by mountain bloc. Preclearance forest follows Hall *et al.* (2009). Per cent gazetted is according to UNEP-WCMC (2009). Human populations are based on LandScan (2006) estimates, corrected according to the protected area data (no people live in National Parks or Game Reserves) and ward-level household surveys from the Tanzanian census (NBS, 2002; Appendix 3, available online at http://www.journals.cambridge.org/enc2011001).

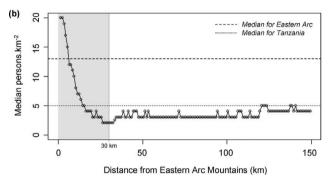| Mountain bloc	Total area (km²)	Base height (m)	Summit height (m)	Mountain forest (km²)			Mountain population		
				Preclearance	Present-day	% Gazetted	Total (10³)	Mean population km⁻²	Median population km⁻²
Taita Hills	941.4	509	2198	–	10.0	30	60	64	25
North Pare	510.3	697	2099	323.0	40.7	52	69	136	35
South Pare	2327.5	459	2454	1088.7	129.9	89	131	56	11
West Usambara	2945.2	290	2294	2362.2	328.4	80	555	188	38
East Usambara	1145.0	123	1501	807.0	384.3	63	96	84	22
Nguu	1562.9	676	1998	667.9	326.7	56	39	25	7
Nguru	2564.9	351	2382	919.9	357.1	76	95	37	10
Ukaguru	3242.6	415	2259	1075.6	191.0	79	142	44	20
Uluguru	3057.3	121	2636	1627.8	308.6	84	219	72	25
Malundwe	32.8	476	1259	24.1	2.3	100	0	0	0
Rubeho	7984.4	272	2345	2647.8	520.9	57	167	21	10
Udzungwa	19 375.3	249	2556	5790.7	1726.3	82	572	30	10
Mahenge	2606.4	320	1501	557.1	20.2	56	52	20	9
All Eastern Arc	48 296.1	121	2636	17 891.6	4346.3	75	2197	45	12
[Including plateaus]	[51 628.2]	[121]	[2636]	[17 891.6]	[4346.3]	[75]	[2353]	[46]	[13]

Figure 5 Human population density versus distance to the Eastern Arc (includes Udzungwa plateaus). (*a*) Peaks in mean density correspond to towns and cities with populations exceeding 100 000. (*b*) Median density better portrays the distribution of rural persons in relation to the mountain resource (0–30 km).

Global typologies derived from digital elevation data provide a welcome platform for large-scale studies of mountain environments and the people they support (Huddleston *et al.* 2003). At more local scales, regional biogeography, naming conventions and micro-relief gain importance, and so targeted case studies are required to obtain relevant delineations of region extent. Here, we provide a consistent topographical foundation for delimiting the Eastern Arc Mountains, one of the world's most important ecoregions for conservation (Olson & Dinerstein 2002). The approach we present is generic and could be readily calibrated for application to other mountain regions.

Mountain ecosystems, like all biological assemblages, are moving targets: the products of ancient evolutionary processes, recent climatic conditions and, in the case of the Eastern Arc, ongoing disturbance by humans, fire and large herbivores such as elephants. Ecoregion extent inferred directly from climate, vegetation and/or land use therefore requires frequent revision in response to new data or changes in those variables. Moreover, if considered independently of surrounding habitats and without historical perspective, contemporary snapshots of forest mosaics and local climates have restricted potential to aid understanding of the system as a whole (Fjeldså & Lovett 1997). In cases where mountainous relief is central to the historical affinities under consideration, boundaries defined by topographical means are in our view

preferable. Here, they provide a geographically coherent framework for monitoring, which is likely to incorporate potentially important but as yet undocumented sites for conservation.

When the Eastern Arc was first proposed as phytogeographically distinct in the 1980s, the biological importance of many of the blocs was unconfirmed. Forests in Rubeho, for instance, having only recently received funding for botanical surveys, have long been undervalued in terms of conservation priority (Doggart *et al.* 2006). Similarly, recent focus in Nguru has revealed a number of species new to science, particularly amongst herpetofauna (Menegon *et al.* 2008). Nguu remains largely unsurveyed, but recent field visits and bioclimatic modelling suggest it too could be rich in species (Platts *et al.* 2010). The majority of forest in eastern parts of Nguru and Nguu are within reserves, but their western outliers remain ungazetted, leaving them open to degradation.

The size of the ecoregion is here defined to be 48 000–52 000 km^2, depending on the inclusion of mid-elevation plateaus in Udzungwa. This is higher than a previous estimate of 37 000 km^2 (Tanzania only) published by the Forestry and Beekeeping Division (Mbilinyi *et al.* 2006), which imposes a lower limit of 500 m elevation, omits the western margins of Udzungwa and includes fewer outlying peaks. In Kenya, we identify the main Taita bloc, plus Mount Kasigau and the Sagalla Hills to the south and east, as well as two lower elevation hills (Maungu and Maktau) known to support locally endemic plant species. The explicit inclusion of these outliers is especially important given the plight of other Taita forests, now restricted to a few remnant patches (Pellikka *et al.* 2009), threatening the persistence of many rare species (Rogo & Oguge 2000). Although furthest from the main bloc, Kasigau forests are relatively undisturbed and so may provide refugia for important flora and fauna (for example Taita White-eye *Zosterops silvanus*; Mulwa *et al.* 2007). Elsewhere, outlying features were identified by the regional mountain typology, but omitted from the current definition because of low relative elevation and lack of data on the presence/absence of characteristic Eastern Arc vegetation. Because new data may yet justify their inclusion, we provide the spatial extents of all identified features (Appendix 1, available online at http://www.journals.cambridge.org/enc2011001).

Although these boundaries were not placed directly according to forest distributions, we did use vegetation data to indicate appropriate terrain parameters. Our estimation of current forest cover at over 4300 km^2 is more than some previous studies, but less than the 5700 km^2 of natural forest proposed by Newmark (2002). Other sources put the figure closer to 3500 km^2 (Mbilinyi *et al.* 2006; Burgess *et al.* 2007 and references therein), but are similar to Newmark's estimate if woodlands are included. The land cover data used here have been iteratively improved during a series of workshops in Tanzania through the Valuing the Arc Programme (http://valuingthearc.org/), and were further corrected for the current application by reference to forest

change estimates, government reports and our own field notes. Unless ground-truthed, all such estimates are subject to uncertainty, especially as regards the distinction between closed woodland and deciduous/degraded forest, which can be easily confused in remotely sensed images. Levels of disturbance and fragmentation in the forest interior are also difficult to assess remotely.

To reduce our reliance on these data, which at best provide a current snapshot of forest distribution, we further considered extrapolations of historical forest cover (Hall *et al.* 2009). Such estimates are not directly applicable as ecoregion boundaries as sediment cores are sparsely distributed and an evidence-based assessment of historical extent is only starting to become possible (Mumbi *et al.* 2008; Finch *et al.* 2009; Finch & Marchant 2011), but they do provide a broad indication of preclearance cover. The fact that our boundaries fully enclose these kinds of estimates suggests that they are well placed to withstand future changes in distribution, at least over timescales relevant for management. If the boundaries were to require adjustment in the future, this could be addressed multilaterally according to the framework presented here.

Genetic evidence from a range of focal taxa shows that Eastern Arc vegetation has persisted over many millions of years. Phylogenetic analysis of the tree *Macaranga capensis* indicates long-term separation of populations on different mountain blocs, but also past connectivity (A. S. Jump, personal communication 2010); species presently restricted to montane areas may have once encroached on tropical lowlands. Strong affinities have also been observed between the flora and fauna of the Eastern Arc and those of west and central Africa, suggesting remnants of a pan-African forest belt (Couvreur *et al.* 2008). More locally, the Lake Nyasa Highlands, Mount Kilimanjaro and coastal forests all contain plant taxa otherwise restricted to the Eastern Arc, as do the Shimba Hills in south-east Kenya, again indicating past connections or possibly long-distance dispersal.

Because of these historical overlaps in composition, the dichotomy of Eastern Arc and coastal vegetation can sometimes be contentious (Burgess & Clarke 2000). An academic reason for maintaining some form of distinction between mountain and coastal vegetation in East Africa is that, since 2004, they have been classified as belonging to different biodiversity hotspots (Eastern Afromontane versus Coastal Forests of East Africa; Mittermeier *et al.* 2004). In addition, the Tanzanian mountains contain central government reserves administered by the catchment forest office, whereas the districts administer coastal forest reserves. From a human perspective, mountain people face different challenges to those living in towns or rural lowlands (Kreutzmann 2001); thus ensuring their social welfare and right to the traditional use of natural resources, whilst also fulfilling conservation objectives, demands a specific focus on the mountain region.

The 500 m threshold for plant endemism, although a pragmatic response to the need for spatially consistent mountain limits, does not account for geographical differences in baseline elevation, nor is it consistent with other taxonomic groups (compare with Poynton *et al.* 2007). Using the altitudinal range of forest within a given mountain bloc is an appealing alternative, but one that is particularly sensitive to recent patterns of deforestation. The spatial limits presented here might be an appropriate basis for a new set of endemism criteria. Our results suggest that well over half of the plant species here tentatively considered 'near-endemic' would be classified as strictly endemic according to the derived ecoregion boundary, and that all could be consistently defined according to an inclusion zone of up to 20 km. Moreover, in a preliminary retabulation of plant endemism, which compares the recorded elevations of specimens with the altitudinal limits of the corresponding mountain blocs (as detailed in Table 2), nearly all 'near-endemics' can be considered strictly endemic. We encourage similar tests for other taxonomic groups (spatial data available online at http://www.journals.cambridge.org/enc2011001).

In providing a spatially explicit definition for this area of endemism, we hope to prompt research and conservation in lesser-studied parts of the Eastern Arc, which could be biologically and politically undervalued due to spatial bias in the data (Platts *et al.* 2010; Ahrends *et al.* 2011). The boundaries are also relevant for reforestation strategies, particularly ahead of the United Nations REDD pilot (http://www.un-redd.org/) in Tanzania.

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Supplementary material

Delimiting tropical mountain ecoregions for conservation

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APPENDIX 1

Description of spatial data for boundary placement

The following spatial files are available online at http://www.journals.cambridge.org/enc2011004. The projection is Africa Albers equal-area conic (WGS 1984 spheroid, central meridian 25E, standard parallels 20N-23S). Boundaries were derived using elevation data from the CGIAR-SRTM DEM (Jarvis *et al*. 2008). For general use, we recommend version [9] because it includes all highland habitats as well as the lowest parts of Matundu forest in Udzungwa. Two alternative coordinate systems are provided: UTM zone 37S and geographic WGS 1984, available online at http://www.journals.cambridge.org/enc2011002 and http://www.journals.cambridge.org/enc2011003, respectively.

	File name (dbf, prj, shp, shx)	Description
[1]	EasternArc_halfdegSquares	56 half-degree grid squares that intersect with the Eastern Arc region. Defines the spatial limits of data in [2-9]
[2]	RegionalMountainTypology	Mountain classification as defined in Appendix 2
[3]	MountainClusters_prominence	Mountainous features from [2] aggregated within simplified bounds. Prominence is summit height minus lowest boundary elevation. Small, isolated fragments not included (< 1 km^2 and > 1 km from nearest neighbour)
[4]	EasternArc_byPart	Eastern Arc boundary definition, according to topographic prominence ($\geq$ 600 m) and phytogeographical divisions described by Lovett (1990)
[5]	EasternArc_byBloc	As in [4], dissolved by mountain bloc
[6]	EasternArc_byBloc_incMikumi	As in [5], retaining Mikumi relief that surrounds Malundwe Mountain
[7]	EasternArc_byBloc_incPlateaus	As in [5], with the addition of mid-elevation plateaus in Udzungwa
[8]	EasternArc_inclusionZones	As in [7], including 10, 20 and 30 km buffer zones around the perimeter. Some lowland remnants of characteristic Eastern Arc forest persist within 10 km (e.g. Magombera); all 'near-endemic' plant taxa (as defined in the main article text) have been collected within 20 km; the density of rural persons is highest within 30 km
[9]	EasternArc_byBloc_incPlateaus&LowMatundu	As in [7], with the addition of low-lying forest in Matundu. This version was created for the Valuing the Arc Programme (http://www.valuingthearc.org/) to investigate ecosystem service provision. It is also used by the KITE project (http://www.york.ac.uk/res/kite/) to assess biodiversity and land cover change, and by Missouri Botanical Garden to investigate the spatial limits of plant endemism.

APPENDIX 2

Mountain classes defined in the regional mountain typology

Mountain classes defined in the regional mountain typology (90 m raster resolution). LER is local elevational range, defined across a circle of 500 m radius. Areas include south-western slopes of Mt. Kilimanjaro and northern parts of the Lake Nyasa Highlands (see file [2]).

Mountain class	Elevational zone	Slope and LER constraints	Area in half-degree grid cells (km²)
1	0–1000 m	$LER_{500\,m} \geq 100$ m	15 890
2	1000–1500 m	Slope > 10° or $LER_{500\,m} \geq 100$ m	13 570
3	1500–2500 m	Slope > 5°	11 579
4	2500–3500 m	No constraint	96
5	3500–4500 m	No constraint	11
6	≥ 4500 m	No constraint	0
7	[Isolated inner basins and plateaus < 25 km² in area]		1913

APPENDIX 3

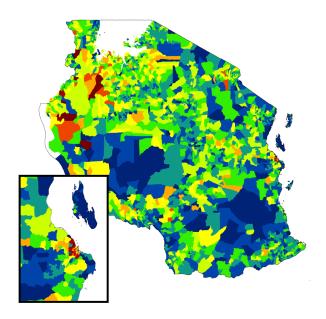## Derivation of the population surface

The distribution of persons at 1 km resolution was based on a modelled population surface, provided by LandScan (LandScan 2006; 30 arc-sec resolution). These estimates were rescaled on a ward-by-ward basis, such that ward totals matched empirical data from the 2002 Tanzania census (NBS 2002). An additional correction was made, such that no person should be permanently resident in a national park or game reserve (World Database on Protected Areas; UNEP-WCMC 2009). It was not appropriate to use previous LandScan releases, closer to the census year, because of errors and shortfalls in those datasets (see http://www.ornl.gov/sci/landscan/). Census data were not available for Kenya, and so population estimates for the Taita Hills were mapped directly from LandScan.
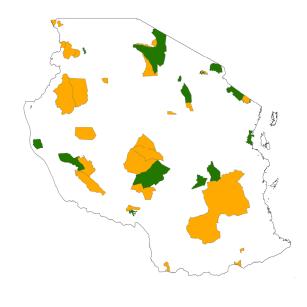
ESRI ArcMap procedure for deriving the high-resolution human population surface in Tanzania

1. Using the total population field in the Tanzania census (2002) shapefile, grid the wards polygon data at 30 arc-sec resolution (WGS1984 coordinate system; Feature to Raster Tool). Let this raster be called 'wardPop02'.

2. Extract national parks and game reserves from the WDPA (2009) shapefile. Grid these polygons at 30 arc-sec resolution and reclassify NoData values such that national parks and game reserves have zeroes and all other cells have ones (Reclassify Tool). Multiply this grid and the LandScan (2006) grid to remove persons from these protected areas (Single Map Algebra Tool). Let the resultant raster be called 'LS06_WDPA'.

3. Using the census ward number as the zone marker, calculate the total 'LS06_WDPA' population in each census ward (Zonal Statistics Tool). Depending on computational power, it may be necessary to perform this operation separately for each region of Tanzania (merge results using Mosaic to Raster Tool). Let the resultant raster be called 'LS06_WDPA_tot'.

4. Using the Single Map Algebra Tool, divide 'LS06_WDPA' by 'LS06_WDPA_tot' (allocate zero values where the quotient is undefined) and multiply by 'wardPop02'. The result is a 30 arc-sec population surface where ward totals match the 2002 census counts, and where no people are resident in game reserves or national parks. Let this grid be called 'popgrid02_dd'.

5. Population density in the form persons.km^{-2} (rather than persons per 30 arc-sec) can be obtained as follows. First, calculate the areas of all 30 arc-sec grid squares in Tanzania. This can be achieved by generating a 30 arc-sec raster in which each cell has a unique value, converting this to polygons, adding an 'area_km2' field to the attribute table (calculate geometry using Africa Albers Equal Area Conic coordinate system), and then converting this shapefile back to raster format (snap to 'popgrid02_dd'). Second, divide 'popgrid02_dd' by the area grid. Finally, project the resultant raster from the geographic coordinate system (WGS 1984) to UTM zone 37S or Africa Albers, using nearest neighbour assignment.

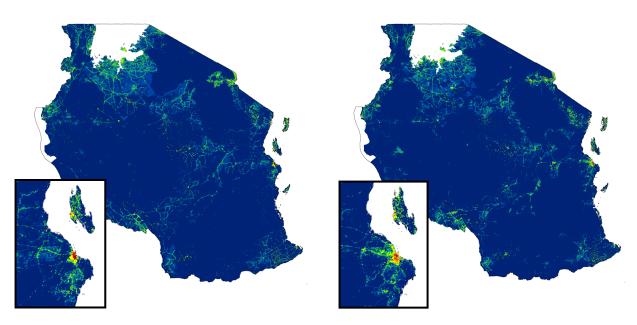**(a) Ward populations, 2002 Tanzania census**

(b) Protected areas where no people live

(c) LandScan 2006, persons.km^{-2}

(d) High-resolution estimates for 2002, persons.km^{-2}

(*a*) Ward populations according to the Tanzania census in 2002. (*b*) Game reserves (orange) and national parks (green) from the World Database on Protected Areas. (*c*) Population distribution according to LandScan 2006. (*d*) As in (*c*) but with cell values adjusted to match the ward census counts and protected area data. Respectively, cool colours (blue-green) and warm colours (yellow-red) correspond to areas of low and high population. Insets show zoomed perspectives of Dar es Salaam and Zanzibar Island.

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