RESEARCH ARTICLE

The Species–Area Relationship and Confounding Variables in a Threatened Monkey Community

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This study investigates the species–area relationship (SAR) for forest monkeys in a biodiversity hotspot. The Udzungwa Mountains of Tanzania are well-suited to investigate the SAR, with seven monkey species in a range of fragment sizes ($0.06–526\,km^2$). We test the relationship between species richness and forest fragment size, relative to human and environmental factors. We distinguish resident and transitory species because the latter have an "effective patch size" beyond the area of forest. Forest area was the strongest (log-linear) predictor of species richness. However, forest area, elevation range and annual moisture index were intercorrelated. Previous knowledge of the relationship between elevation and tree communities suggests that the SAR is largely a result of habitat heterogeneity. Isolation by farmland (matrix habitat) also had a significant negative effect on species richness, probably exacerbated by hunting in small forests. The effect of area and isolation was less for transitory species. The human influence on species' presence/absence was negatively related to the extent of occurrence. Weaker relationships with temperature and precipitation suggest underlying climatic influences, and give some support for the influence of productivity. A reduced area relationship for smaller forests suggests that fragment sizes below $12–40\,km^2$ may not be reliable for determining SAR in forest monkeys. Further practical implications are for management to encourage connectivity, and for future SAR research to consider residency, matrix classification and moisture besides precipitation. Am. J. Primatol. 72:325–336, 2010.   © 2009 Wiley-Liss, Inc.

Key words: eastern arc; fragmentation; island biogeography; niche; tropical forest

INTRODUCTION

While evidence for the species–area relationship (SAR) is widespread [Lomolino, 2000], there are many confounding factors that have yet to be fully evaluated [Debinski & Holt, 2000; Ross et al., 2002; Williamson, 1989]. Diurnal primates offer an opportunity to test the SAR as they are conspicuous, easily identifiable and they live in highly fragmented habitats. Nearly half of the world's primate taxa are threatened with extinction, with 38% of taxa at risk in Africa, primarily through deforestation [IUCN, 2009]. Repeated studies have shown the reduced primate species richness with forest loss and isolation [Cowlishaw, 1999; Harcourt & Doherty, 2005; Reed & Fleagle, 1995].

The simplest explanation for the SAR is that an increase in area statistically increases the likelihood of occupancy [Connor & McCoy, 1979; Whittaker, 1998]. Alternatively the relationship may result from the dynamic equilibrium between immigration and extinction [McGuinness, 1984; Whittaker, 1998] affected by area and isolation. Species richness in various locations has also been related to habitat heterogeneity, productivity/rainfall, elevation/temperature and biogeography [Cowlishaw & Dunbar, 2000; Kay et al., 1997; Lawes & Eeley, 2000; Reed & Bidner, 2004; Reed & Fleagle, 1995]. Many consider habitat heterogeneity to be the main driver of SARs, because large areas tend to have a greater diversity of habitats [Báldi, 2008; Tews et al., 2004], but few have investigated these relationships for primates and the influence of

habitat remains ambiguous [Lehman, 2004]. Most primate species–area studies have incorporated few covariates and human disturbance is often overlooked. In Amazonia the impact of disturbance on species presence is greater than the impact of habitat fragment size [Michalski & Peres, 2005]. The impact of fragmentation on species richness has also been exacerbated by hunting in Amazonia and West Africa [Brashares et al., 2001; Peres, 2001], canopy loss in Kenya [Anderson et al., 2007a] and human density around 169 small African reserves [Harcourt et al., 2001].

The Udzungwa Mountains of Tanzania have great potential for investigating the SAR. With 13 species, the Udzungwa primate community is one of the most important for conservation in the continent [Butynski et al., 1998; Jones et al., 2005; Rovero et al., 2009]. The area has around 1,600 km^2 of forest in a 10,000 km^2 area, including around 550 km^2 of closed-canopy forest (excluding Mufindi to the west and Image to the north). The Udzungwas also have a wide range in patch sizes and levels of isolation (e.g. 22 fragments: size 0.06–526 km^2, median 6.1 km^2; distance between 0.1 and 120 km, median 36.1 km). A previous study of East African primates (Uganda) did not find a SAR among smaller, less isolated fragments [Onderdonk & Chapman, 2000: size 0.008–1.3 km^2, mean 0.1 km^2; distance between 50 and 300 m]. Insufficient isolation was also cited for the lack of a SAR in a meta-analysis for Africa [Harcourt & Doherty, 2005: size 0.01–51 km^2, median 0.2 km^2; distance between 0.1 and 53 km, median 2 km].

Previous studies have demonstrated human and environmental influences on the Udzungwa primates. The endemic Udzungwa red colobus (*Procolobus gordonorum*) has reduced density and group size in degraded and high elevation forests [Marshall, 2007; Rovero et al., 2009]. Hunting is also associated with the absence or reduction of mammals in some highland Udzungwa forests [Nielsen, 2006; Topp-Jørgensen et al., 2009] and in the southern Uzungwa Scarp Forest Reserve [Rovero, unpublished data]. No published research exists on the effects of patch size on Udzungwa primates; however, a positive relationship was found between mammal species richness and fragment size in six forests [Jørgensbye, 2004]. The presence of black and white colobus was also related to forest size in the nearby coastal forests of Kenya [Anderson et al., 2007a].

Here we investigate the SAR for seven monkey species incorporating more potentially confounding variables, a broader range of forest sizes and greater isolation than previous studies in African forests. Our objectives are to assess the presence and form of the SAR, to determine the potential causal factors and to provide useful information for conservation management.

METHODS

Study Areas and Species

We derived estimates of size and habitat type for 22 Udzungwa forest fragments from Landsat imagery (Landsat ETM+; Global Land Cover Facility/ US Geological Survey; Oct 25 and Nov 1, 1999; Paths 167–8; Rows 65–6; Fig. 1; Table I). Forest degradation within most fragments has resulted in varying proportions of open-canopy (heavily disturbed) and closed-canopy forest (Table I). We verified canopy cover for about 50% of the forest area from ground survey and aerial overflights. The elevation range of fragments was 269–2,520 m (SRTM DEM; http:// srtm.usgs.gov/; Table I).

Some of the forest sizes given in Table I are smaller than previous estimates [Dinesen et al., 2001; Government of the United Republic of Tanzania, 1983; Lovett & Pócs, 1993]. Deforestation and pitsawing in the uplands of Kisinga-Rugaro, Iyondo and Dabaga, removed around 63 km^2 of forest. Limited increase in forest cover was also seen along the eastern side of Magombera forest (11.89 km^2 from 8.55 km^2 in the 1980s). We found that 1:50,000 topographical maps [Government of the United Republic of Tanzania, 1983] misclassified some areas of woodland and bamboo as forest. While the habitat classification presented is a work in progress (e.g. bamboo cover in Uzungwa Scarp forest remains unmeasured and topography is not accounted for), we feel that the forest cover estimates are sufficiently accurate for this study.

Seven monkeys known from the range are the Udzungwa red colobus, Angolan black and white colobus (*Colobus angolensis palliatus*), Sykes' monkey (*Cercopithecus mitis* ssp.), vervet monkey (*Cercopithecus aethiops rufoviridis*), yellow baboon (*Papio cynocephalus cynocephalus*), Sanje mangabey (*Cercocebus* [*galeritus*] *sanjei*) and the kipunji monkey (*Rungwecebus kipunji*). Three species are endemic to southern Tanzania and are of international importance for conservation (*R. kipunji*—critically endangered; *C. g. sanjei*, *P. gordonorum*—both Endangered; [IUCN, 2009]).

Data Collection

Here we summarize 30 years of monkey surveys in the Udzungwa Mountains [Dinesen et al., 2001; Ehardt et al., 1999; Jones et al., 2005; Lovett & Pócs, 1993; Rodgers, 1981; Topp-Jørgensen et al., 2009], plus unpublished records of species presence accumulated during our surveys of forest status, species composition and monkey group/transect counts. These surveys had good coverage (Table I), so it is unlikely that species were overlooked.

We supplemented the existing data on monkey species presence with surveys conducted between 1999 and 2009 by Marshall (Matundu [126 days], Ndundulu [94], Mwanihana [111], Nyumbanitu [35],
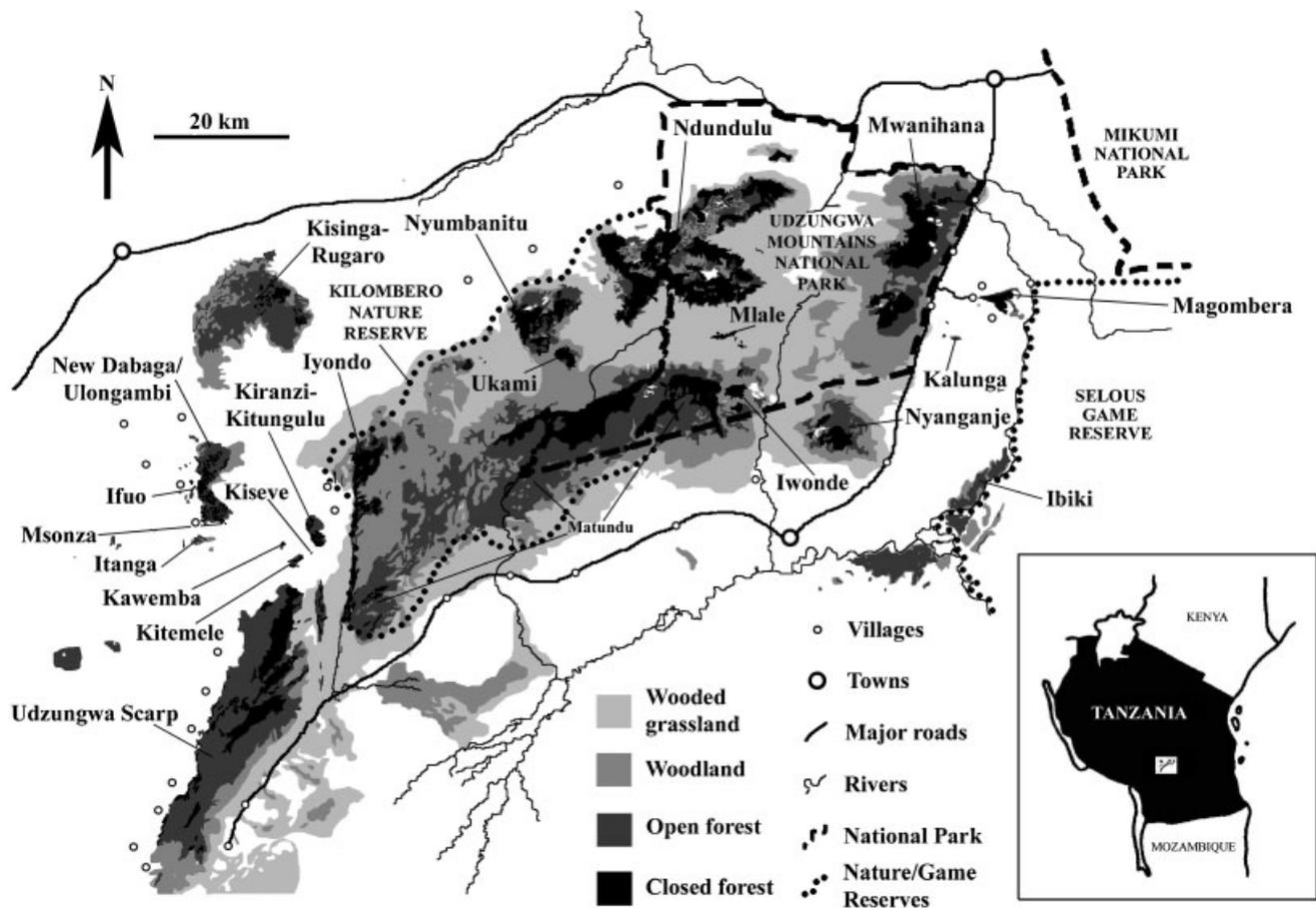
Fig. 1. Habitat map of the Udzungwa Mountains based on Landsat imagery. Areas of unclassified habitat are mostly agriculture and bushland, with dry *Commiphora* and *Acacia* woodland in the north. The map excludes Mufindi forests to the west and Image to the north.

New Dabaga/Ulongambi [47], Magombera [68], Iyondo [14], Kalunga [11] and Msonza [6]), Jørgensbye (Kiranzi-Kitungulu, Kitemele, Kawemba, Ifuo, Itanga, Kiseve and Msonza [16 days each]), and Rovero (Mwanihana [100], Uzungwa Scarp [30], Matundu [12] and Iyondo [7]). The total number of days spent in each fragment including our surveys, the literature and personal communications, was approximately proportional to the size of each forest (Table I). The forests of Ukami and Iwonde were visited by Marshall for 5 and 2 days, respectively. Because of their small size, existing literature [Lovett & Pócs, 1993 1 day in each forest; Iwonde: Ehardt et al., 1999 3 days; Ukami: Dinesen et al., 2001 10 days] and the absence of problematic transitory species, these visits were adequate to determine the resident species. We determined the presence of species in Kisinga-Rugaro forest from the literature [Lovett & Pocs, 1993 5 days; Dinesen et al., 2001 and Dinesen, personal communication 66 days; Jones, 2008 16 days].

Unlike previous studies, we classified species based on their residency in a fragment, because some species used habitats beyond the forest. We considered monkeys to be "transitory" if found only at the outer limits of a fragment, where the forest met the adjacent matrix habitat. Species were assumed to be "resident" if a social group was located in the interior of a fragment, with no evidence of leaving the fragment. Residency was usually obvious because of the presence of multiple groups and known behavior of the species concerned (e.g. forest-dependence). Transitory species were mostly baboons or vervet monkeys, which are typically woodland or bushland species. In Kalunga forest, one black and white colobus group was transitory because it fed in an adjacent rubber (*Hevea brasiliensis*) plantation. Fragments with species that were only transitory and/or represented by single individuals were rare. We repeated our analyses using the same number of variables, both with and without the transitory species.

We were mostly confident on the residency of monkeys; however, there were some uncertainties resulting from undersampling in four fragments: Ibiki (visited for only 1 day by Marshall and 1 day by Thomas Struhsaker), Nyanganje (3 days [Abel Mtui, personal communication]) and Mlale (1 day [Ehardt

TABLE I. Description of 22 Forest Fragments in the Udzungwa Mountains

Forest	Size (km²)	Closed (km²)	Elevation (m)	Monkey hunting	Sample days	% surveyed	R. kip.	C. sanj.	P. gord.	C. ang.	C. mitis	P. cyn.	C. aeth.
Matundu	526.32	118.11	279–1,046	Low	257	62	–	–	x	x	x	x	–
Udzungwa Scarp	314.48	79.22	290–2,144	High	122	70	–	x	x	x	x	o	o
Ndundulu	230.64	161.10	1105–2520	Low	559	85	x	–	x	x	x	–	–
Mwanihana	150.59	69.37	351–2,263	Low	576	95	–	x	x	x	x	o	–
Kisinga-Rugaro	116.25	9.31	1,627–2,322	High	87	80	–	–	–	x	x	–	–
Nyumbanitu	56.52	27.92	1,074–2,322	Low	134	85	–	–	x	x	x	–	–
Iyondo	43.17	27.92	814–1,850	Low	24	80	–	–	x	x	x	–	–
Nyanganje	41.92	13.28	350–1,038	Low	3	30	–	–	x	x	x	o/–	o/–
New Dabaga/Ulongambi	39.97	16.02	1,764–2,081	High	110	95	–	–	x	x	x	–	o
Ibiki	16.91	0.00	250–277	Low	2	40	–	–	x	x	x	x/o	–
Magombera	11.89	6.85	269–302	Low	396	90	–	–	x	x	x	o	o
Kiranzi-Kitungulu	9.10	4.42	1,525–1,922	Low	18	57	–	–	x/–	x	x	–	–
Ukami	7.18	5.40	902–1,651	Low	16	70	–	–	x	x	x	–	–
Iwonde	4.97	4.97	980–1,472	Low	6	70	–	–	x	x	x	–	–
Kitemele	2.54	1.20	1,431–1,766	High	17	75	–	–	–	–	x	–	–
Mlale	2.18	2.18	1,112–1,308	Low	1	20	–	–	x	x	x	o/–	–
Kawemba	0.57	0.23	1,557–1,702	High	17	100	–	–	–	–	x	–	–
Ifuo	0.57	0.11	1,920–2,041	High	17	90	–	–	–	x	x	–	–
Itanga	0.42	0.0	1,804–2,030	High	16	100	–	–	–	–	–	–	o
Kiseve	0.22	0.22	1,496–1,543	High	16	100	–	–	–	–	x	–	–
Kalunga	0.1	0.0	281–299	Low	17	100	–	–	x	o	1	o	–
Msonza	0.06	0.06	1,816–1,846	High	22	100	–	–	–	x	–	–	–

Survey effort includes all sources used. See text for sources and full latin names. Monkey species presence is indicated by x (resident), o (transitory), – (absent), or 1 (solitary individuals only).

et al., 1999]). Finally, an area of Kiranzi-Kitungulu forest rumored to contain red colobus was searched for only 1 day. Because of the uncertainties we repeated the relevant analyses for both the presence and absence of uncertain species in the under-sampled fragments. The most uncertain fragments were excluded from the main analyses (Ibiki for resident species; Nyanganje for resident and transitory species combined).

In addition to the forest area, we tested species richness against 16 other explanatory (predictor) variables that have previously been associated with primate diversity/abundance or plant community composition. Using the habitat classification (Fig. 1) we included the proportion of open-canopy forest as an indicator of habitat degradation. We also used two measures of isolation employed previously in species–area studies, namely the mean shortest distance (from edge to edge) to all other forest fragments and distance to the nearest larger fragment. Because of the importance of the intervening ''matrix'' habitat for transfer between fragments [Andrén, 1994], we also included isolation by farmland as a binary variable. We considered fragments to be ''isolated'' if separated from all other fragments by farmland, or ''not isolated'' if separated by uncultivated land (e.g. grassland, bushland or woodland).

We defined the level of hunting as either low or high (Table I). Hunting was considered ''high'' in fragments surrounded by villages with known monkey hunters and where we observed snares daily. We considered hunting to be ''low'' for all other fragments, where we recorded evidence of hunting on no more than two occasions. We confirmed this dichotomy of hunting levels from 20 years of close association with the local people. The relative levels of hunting are also supported by previous research and personal observations [Nielsen, 2006; Rodgers et al., 1980; Topp-Jørgensen et al., 2009; Nielsen, personal communication]. We saw no evidence that hunting levels had changed over the study period. The presence of snares alone was not considered sufficient evidence for monkey-hunting as snares are often set for other animals. Most hunting occurred in the western forests in areas dominated by the Hehe tribe that eats monkey meat.

We obtained climate surfaces from the Centre for Resource and Environmental Studies (Australian National University, http://fennerschool.anu.edu.au/) and downscaled them to 100 m by interpolation of regression parameters across a high-resolution digital elevation model [Platts et al., 2008]. For each fragment we used the minimum, maximum and range of annual precipitation and temperature across grid cells. Because the amount of rainfall in the driest month can be important for determining plant species distribution [Platts et al., 2008], we also used the minimum and maximum precipitation from the driest month for each fragment.

A further climate variable that is commonly related to plant distribution is the annual moisture index (AMI), an indicator of moisture availability resulting from the decreased evapo-transpiration and the increased cloud cover with elevation. It is the ratio of mean annual precipitation to potential evapo-transpiration [Thornthwaite, 1948]. Since AMI range is very closely related to elevation range (Pearson correlation: $r = 0.91$), to avoid redundancy we excluded elevation as a predictor variable, instead using minimum, maximum and range in AMI from the 100 m cells in each forest fragment. Elevation is the strongest predictor of plant species turnover in the Udzungwa Mountains [Lovett et al., 2006] and hence AMI range of a fragment is a good proxy for habitat heterogeneity.

Our research complied with protocols approved by the University of York Animal Care and Use Committee and adhered to Tanzanian law.

Statistical Analyses

We first employed univariate tests of Spearman's rank correlation for each variable vs. species richness (or Wilcoxon rank sum tests for binary variables). We use the Hochberg correction [Hochberg, 1988] for all univariate analyses throughout, to adjust for repetitive testing. To improve the linearity and skew for subsequent modelling, we applied natural logarithmic ($\log_n$) transformations to the variables forest area, distance to nearest larger fragment, and maximum AMI. Because of extreme skew in AMI range, we applied square root transformation, then $\log_n$ transformation. We used generalized linear models (GLMs) to assess the multivariate (multiple predictor variable) relationships between species richness and the 17 variables, using Poisson error and log link functions (R statistical package, version 2.9.0; http://cran.r-project.org/).

To promote parsimony and to mitigate the confounding effects of collinearity in model selection [Crawley, 2005], we first tested predictor variables for intercorrelation using Pearson's coefficient (r). We considered collinearity to be serious if $|r| \geq 0.7$ [Schadt et al., 2002]. In such cases we retained the variable that yielded the best univariate model, resulting in a set of nine independent variables eligible for stepwise selection (Table II footnote). We calibrated an additional GLM using AMI range in place of forest area, to investigate the relative modelling potential of these two highly correlated variables. We reduced the variables in the GLM using combined backward and forward stepwise selection, removing or adding variables according to the Akaike Information Criterion (AIC). We considered the influence of potential outliers in the GLM to be serious if Cook's Distance was near to or greater than 1.0 [Maindonald & Braun, 2003]. We checked the full GLM for curvature by using quadratic terms

TABLE II. Predictors of Resident Species Richness in 21 Udzungwa Forest Fragments at the 95% (and 90%) Level

Significant variables	Test statistics	P
Spearman and Wilcoxon rank: 95% $\alpha = 0.0039$, 90% $\alpha = 0.0077$		
Forest area[+]	$r_s = 0.846$	<0.0001
AMI range[+]	$r_s = 0.833$	<0.0001
Isolation by farmland [−]	$W = 104.0$	0.0004
Minimum AMI[−]	$r_s = -0.691$	0.0005
Maximum temperature[+]	$r_s = 0.654$	0.001
(*Maximum precipitation*[+])	($r_s = 0.558$)	(*0.009*)
(*Hunting*[−])	(*W = 87.0*)	(*0.016*)
Multivariate stepwise GLM (both datasets resulted in just one variable)		
[a]Log$_n$ forest area[+]	AIC = 64.76, %D = 60.26	0.004
[b]Log$_n$ $\sqrt{}$AMI range[+]	AIC = 65.82, %D = 53.13	0.005
Univariate GLM excl. area and AMI range: 95% $\alpha = 0.0083$, 90% $\alpha = 0.025$		
Isolation by farmland[−]	AIC = 66.23, %D = 50.40	0.008
(Minimum AMI[−])	(AIC = 67.68, %D = 40.67)	(0.013)
(Maximum temperature[+])	(AIC = 67.90, %D = 39.21)	(0.020)

Near-significant predictors ($P \leq 0.02$) are shown in italics. "%D" = percent deviance explained ($100 \times [1 - \text{residual deviance/null deviance}]$); "+", positive trend; "−", negative trend.
[a]Variable set 1: log$_n$ forest area, hunting, mean distance to all fragments, log$_n$ distance to larger fragment, isolation by farmland, canopy loss, minimum precipitation, minimum AMI, log$_n$ maximum AMI.
[b]Variable set 2: As set 1 but replacing log$_n$ forest area with log$_n$ square root AMI range.

[Crawley, 2005]; however, the reduced model fit suggested linear models were appropriate.

We consider all significant models within two AIC values of the final stepwise model to be equally good at explaining variation in species richness [Burnham & Anderson, 2003; Kamilar & Paciulli, 2008]. We therefore ran additional GLM analyses for comparison with the stepwise GLM. First, we employed the univariate GLM analyses for the significant and near-significant predictors from Spearman/Wilcoxon tests. Second, we ran GLMs using log$_n$ forest area together with each of the variables in turn. Probability values (P) were used to interpret the relationships, and all tests were two-tailed. Given concerns regarding dichotomous significance testing [e.g. Fidler et al., 2006], we considered variables to be strong predictors if GLM and Spearman/Wilcoxon tests were in agreement at the 95% level, and weak at the 90% level. Because of the conservative nature of endpoint adjustment [Moran, 2002], we present tentative ("near-significant") results where P was less than or close to 0.05 prior to the Hochberg correction.

We also tested the presence/absence of each species that was resident in at least four fragments vs. the 17 predictor variables. Yellow baboons were too scarce, so we used both resident and transitory records for this species. We employed Student's t-tests to evaluate differences in the means of 15 predictor variables (all parametric following transformation) for fragments in which each species was present vs. absent. For the two binary variables (hunting and isolation by farmland), we tested for the difference

in Cohen's Kappa (κ) (epiKappa function of epibasix package; http://cran.r-project.org/). We did not attempt multivariate analyses (e.g. stepwise logistic regression) because of insufficient degrees of freedom.

To investigate the fragment size range required for investigating the SAR, we repeated the univariate GLM analysis of species richness vs. log$_n$ forest area excluding each fragment in turn, beginning with the largest. Given the high level of fragmentation that has occurred in the tropics we assume that small fragments are much more common and therefore do not test the minimum required fragment size.

Finally, to investigate the influence of human disturbance independently from area, we compared species richness of the smallest forests ($<12 \, \text{km}^2$) that were hunted and isolated by farmland vs. those that were not. We used Wilcoxon tests and a GLM of species richness vs. log$_n$ forest area and an isolation:hunting interaction term.

RESULTS

Species Richness

We recorded six resident species in the forest fragments (range 0–4 species per fragment, median 3.0; Table I). Univariate tests show that high-resident species richness relates most strongly to large forest area, followed by high AMI range, lack of isolation by farmland, low minimum AMI and high maximum temperature (Table II). High maximum annual precipitation, low levels of hunting, high maximum precipitation in the driest month, low

temperature range and high precipitation range were near-significant predictors of high-resident species richness ($0.47 \leq |r_s| \leq 0.56$, $0.008 \leq P \leq 0.051$, $N = 21$, Hochberg 90% $\alpha = 0.0077$). Red colobus were not found in Kiranzi-Kitungulu, despite past documentation (<3 individuals per km^2; Dinesen et al., 2001).

Four of the five predictors of resident species richness remained significant at the 95% level when we included transitory species, while maximum annual precipitation and maximum precipitation in the driest month also showed the positive trends ($|r_s| \geq 0.61$, $P \leq 0.0031$, $N = 21$, $\alpha = 0.0042$). Unlike analyses based on only resident species; however, AMI and maximum temperature emerged as marginally stronger predictors than area ($r_s = 0.77$, 0.734 and 0.727) and temperature and precipitation range were significant at the 90% level ($r_s = -0.59$ and 0.57, $P = 0.0047$ and 0.0070, $N = 21$, $\alpha = 0.01$). Only a near-significant relationship was found between isolation of forest fragments by farmland and species richness ($W = 86$, $P = 0.0220$, $N = 21$).

From Pearson correlation between the predictor variables we found that log$_n$ forest area correlated with log$_n$ square root AMI range (and hence elevation range; $r = 0.89$). The eight temperature and precipitation variables were also highly intercorrelated (mean $|r| = 0.83$). Hunting also correlated with five of the temperature and climate variables (maximum annual precipitation $r = -0.81$; maximum temperature $r = -0.75$; maximum precipitation driest month $r = -0.74$; temperature range $r = 0.72$).

From stepwise GLM, we found that resident species richness per forest fragment was best modelled using log$_n$ forest area alone (Table II). Repeating the stepwise GLM with log$_n$ square root AMI range in place of log$_n$ forest area, produced a significant but weaker univariate model (Table II). Univariate GLMs for other predictor variables found only one comparable model (isolation by farmland; Table II). Models were not significant for log$_n$ forest area with any second variable (AIC ≥ 66.74, $P \geq 0.14$, $N = 21$).

GLMs for species richness including both resident and transitory species revealed a negative relationship to minimum AMI and the positive relationships to maximum temperature and log$_n$ forest area (AIC = 70.60, 70.67 and 71.36, $P \leq 0.006$, $N = 21$, 95% $\alpha = 0.008$). Unlike resident species, isolation by farmland and log$_n$ square root AMI range were significant only at the 90% level (AIC = 75.22 and 72.76, $P = 0.044$ and 0.010, $N = 21$, $\alpha = 0.1$), while maximum precipitation (annual and driest month), precipitation range, temperature range, hunting, log$_n$ distance to nearest larger fragment and minimum precipitation were significant at the 90% level (AIC ≤ 76.53, $P \leq 0.098$, $N = 21$).

Repeating Spearman/Wilcoxon analyses using alternative scenarios for uncertain fragments (resident baboons in Ibiki and red colobus in Kiranzi-Kitungulu; transitory baboons in Nyanganje and Mlale) we found the same predictors at the 95% level ($P \leq 0.0033$, $N = 22$). Hunting also negatively related to resident species richness at the 90% level ($W = 0.0078$, $P = 0.004$, $N = 22$, $\alpha = 0.0083$) and the influence of temperature range strengthened for resident and transitory species combined ($r_s = 0.61$, $P = 0.0026$, $N = 22$, 95% $\alpha = 0.0045$). GLM analyses for alternative scenarios found one significant model at the 95% level for resident species (log$_n$ forest area: AIC = 69.24, $P = 0.004$, $N = 22$, $\alpha = 0.006$) and four models at the 90% level (isolation by farmland, maximum temperature, minimum AMI and log$_n$ square root AMI range: AIC ≤ 72.92, $P \leq 0.024$, $N = 22$, $\alpha = 0.025$). Significant GLM variables for resident and transitory species combined were unchanged for the alternative scenarios; however, the influence of maximum precipitation, log$_n$ square root AMI range and maximum precipitation in the driest month strengthened (AIC ≤ 77.28, $P \leq 0.012$, $N = 22$, 95% $\alpha = 0.017$).

The analyses suggest a log-linear relationship between species richness and area (Fig. 2A). Using an untransformed x-axis, we felt that Matundu forest
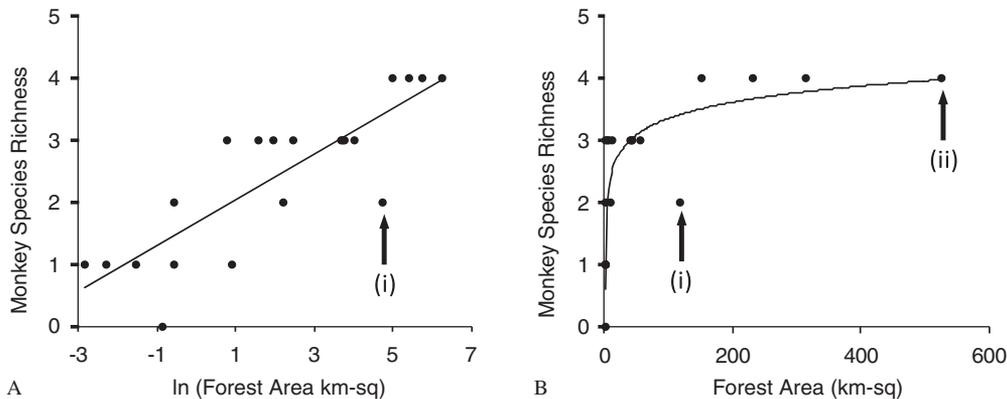

Fig. 2. Scatterplots showing the logarithmic relationship ($r_s = 0.864$, $P < 0.0001$, $N = 21$) between forest area and resident monkey species richness, using (**A**) log$_n$ x-axis, and (**B**) untransformed x-axis. Arrows indicate outliers (i) Kisinga-Rugaro forest, which is more isolated and more heavily hunted than other large forests, and (ii) Matundu forest, which has more deciduous habitat than the other large forest fragments.

may have had a strong influence on the shape of the relationship, because it has the same species richness as forests less than half its size (Fig. 2B). Kisinga-Rugaro forest also appears as an outlier below both trendlines. However Cook's Distance values were all below 0.5, suggesting that no particular point had undue influence on the species–area trend.

From repeated univariate GLMs by successive omission of the largest fragments, we found that the resident SAR was significant at the 95% level until the sample included fragments no larger than $12\,km^2$ (range 0.06–11.89 km^2, median 1.38 km^2, AIC = 35.73, $P = 0.061$, $N = 12$) and only narrowly significant including the next largest fragment of $39.97\,km^2$ (median 2.18 km^2; AIC = 38.91, $P = 0.043$, $N = 13$).

The Presence/Absence

Red colobus presence related to high maximum temperature and precipitation, low minimum AMI, high maximum precipitation in the driest month, high precipitation and temperature range, high minimum precipitation and high log$_n$ square root AMI range at the 95% level (Table III). Red colobus presence is also related to high minimum temperature, high minimum precipitation in the driest month and large forest area at the 90% level (Table III), with a near-significant negative relationship to hunting ($\kappa = 1.69$; $P = 0.046$, $N = 21$). Red colobus occurred in only two of the hunted forests,

TABLE III. Predictors of Presence of Monkey Species in Udzungwa Forest Fragments at the 95% (and 90%) level

Significant variables	t	P
Udzungwa red colobus: 95% $\alpha = 0.0045$, 90% $\alpha = 0.014$, $N = 21$		
Maximum temperature[+]	6.27	<0.0001
Maximum precipitation[+]	5.95	<0.0001
Minimum AMI[−]	4.84	<0.0001
Max precipitation driest month[+]	4.68	0.0003
Precipitation range[+]	4.08	0.0001
Minimum precipitation[+]	3.12	0.0014
Temperature range[+]	3.91	0.0025
Log$_n$ $\sqrt{}$AMI range[+]	3.28	0.0041
(Minimum temperature[+])	(3.06)	(0.0067)
(Min precipitation driest month[+])	(2.91)	(0.0088)
(Log$_n$ forest area[+])	(2.74)	(0.011)
Angolan black and white colobus: 95% $\alpha = 0.00294$, $N = 22$		
Log$_n$ forest area[+]	4.91	0.0002
Sykes' monkey: 95% $\alpha = 0.00294$, $N = 22$		
Log$_n$ forest area[+]	6.11	0.0009
Yellow baboon: 95% $\alpha = 0.0031$, 90% $\alpha = 0.0067$, $N = 21$		
Maximum temperature[+]	5.55	0.00002
Maximum precipitation	3.86	0.0017
(Minimum AMI[−])	(4.08)	(0.0047)

"+", positive trend; "−", negative trend.

both of which were large (Table I). Only three out of eight isolated fragments contained red colobus, compared with all 12 that were not isolated. However, we found that isolation by farmland was not significantly related to red colobus presence ($\kappa = 1.42$; $P = 0.077$, $N = 21$). Repeating the analyses classifying red colobus as resident in Kiranzi-Kitungulu produced the same seven significant variables ($|t| \leq 6.63$, $P \leq 0.0035$, $N = 22$, 95% $\alpha = 0.0045$), with hunting negatively related to red colobus at the 90 % level ($\kappa = 2.237$, $P = 0.013$, $N = 22$, $\alpha = 0.017$), and positive relationships for log$_n$ square root AMI range, minimum temperature, precipitation in the driest month and log$_n$ forest area ($3.02 \leq |t| \leq 3.26$, $P \leq 0.012$, $N = 22$).

There were fewer significant predictor variables for Angolan black and white colobus and Sykes' monkey, with only log$_n$ forest area positively related to the presence of these two species (Table III) and a near-significant positive relationship to log$_n$ square root AMI range ($t = 3.22$ and 4.04, $P = 0.0085$ and 0.0096, $N = 22$, 90% $\alpha = 0.0059$). Unlike the other species, yellow baboon presence did not relate negatively to human variables, even showing a near-significant positive relationship to canopy loss ($t = 3.11$, $P = 0.0112$, $N = 21$, 90% $\alpha = 0.0071$). Baboon presence also related to high maximum temperature and precipitation at the 95 % level and low minimum AMI at the 90% level (Table III). Repeating the analyses with baboons classified as present in the fragments of Nyanganje and Mlale, we found the same top two predictors, but a positive relationship to minimum precipitation, precipitation range and maximum precipitation in the driest month at the 95% level ($t \geq 3.75$, $P \leq 0.002$, $N = 22$, $\alpha = 0.004$) and temperature range at the 90% level ($t = 3.20$, $P = 0.007$, $N = 22$, $\alpha = 0.008$).

Small Fragments

The six small forests ($<12\,km^2$) that were both heavily hunted and isolated by farmland had fewer resident species than the six other small forests ($W = 3.5$, $P = 0.018$). Resident species richness in the nine small isolated fragments was also significantly less than in the three small fragments that was not isolated ($W = 2.5$, $P = 0.024$). No small fragments were hunted but not isolated. The species most affected by hunting in the smaller fragments was the red colobus, which was absent from the all of the small forests that had high hunting, yet present in five of the remaining six small forests (Table I). Black and white colobus were also absent from four of the small, hunted fragments. The effect of isolation by farmland in small fragments that were not hunted was less strong, as two fragments contained red colobus and three contained black and white colobus. A GLM including log$_n$ forest area

and isolation–hunting interaction did not improve on previous models (AIC = 69.60, $P = 0.45$, $N = 21$).

DISCUSSION

We conclude that forest area is the strongest predictor of species richness in forest fragments of the Udzungwa Mountains. The observed log-linear relationship is typical for primates [Cowlishaw & Dunbar, 2000]. Only the four largest fragments sustain resident populations of large papionins (baboons, mangabey and kipunji; Table I), and the presence of two (perhaps three) out of the four most common monkeys is related to forest fragment size (Table III).

We suggest that fragment size must reach at least $12\,km^2$ (median $1.38\,km^2$), but preferably $40\,km^2$ (median $2.18\,km^2$), to determine the SAR for forest monkeys. Fragments must also be sufficiently isolated so that monkeys cannot regularly move between them. Monkeys of similar size to those studied here can disperse outside of forest habitats by up to $4\,km$ [Anderson et al., 2007b]. Harcourt and Doherty [2005] cited limited isolation as a reason for a lack of SAR in their recent meta-analysis for Africa, but a second probable reason is the scale of the study. When incorporating multiple areas, the large variation in the basic requirements of different communities and habitats is overlooked.

Confounding Variables for the SAR

Several factors have likely led to the observed SARs. Although the 16 additional human and climatic variables did not add explanatory power to the SARs in multivariate models, we now discuss how our univariate tests suggest that some of these have contributed to the observed species distributions.

There is strong evidence that AMI is a previously overlooked predictor of resident species richness in primates (Table II). AMI provides information on moisture availability beyond that provided by precipitation alone. A high range in moisture would indicate a broad range of environmental conditions, potentially allowing more monkey species to co-exist. Moreover, the observed positive relationship between forest area and AMI range ($r = 0.89$) and hence elevation range suggests habitat heterogeneity is a major cause of the SAR.

The influence of habitat heterogeneity on the SAR is supported by previous studies on several taxa [Báldi, 2008; Hill et al., 1994; Kallimanis et al., 2008]. Matundu forest, which has no more monkey species than forests half its size, illustrates the influence of habitat heterogeneity (Fig. 2). Matundu is the largest forest fragment in the Udzungwa Mountains ($526\,km^2$), yet it has a low elevation range that is dominated by semi-deciduous lowland forest. It has also been heavily disturbed by logging and elephants, which have encouraged growth of tangled climbers

that prevent regeneration of canopy trees [Marshall, 2007]. Thus, Matundu has lower productivity than other large forests, as tree growth (and thus accumulation of biomass) is limited by restricting vegetation, as seen in other forests of East Africa [Duncan & Chapman, 2003; Marshall, unpublished data]. Matundu has also been slightly less well explored than other large forests (Table I); however, the unvisited areas are dominated by heavily disturbed forest, unlikely to be suitable for the rarer monkeys.

Traditional theory that species richness is related to productivity [Kay et al., 1997; Reed & Fleagle, 1995] has some support from relationships seen between species richness and various measures of precipitation when incorporating transitory species ($P \leq 0.003$). However, precipitation is not a strong predictor in our study as the GLM relationship for transitory and resident species was significant only at the 90% level, and was not significant for all analyses of resident species richness ($0.014 \leq P \leq 0.098$).

The farther a habitat island lies from another, the less likely it is to be colonised [MacArthur & Wilson, 1967]. Accordingly isolation by farmland had comparable AIC scores to both forest area and AMI range (Table II) and hence is one of the strongest predictors of resident species richness in the Udzungwa Mountains. The lack of significant results for the two measures of isolation distance suggests that the matrix habitat is more important than distance. A matrix habitat dominated by farmland implies reduced native vegetation, cover, and food [Anderson et al., 2007b; Marsh, 2003]. Future studies of species distribution may therefore benefit from including a categorical classification of matrix habitat as a predictor. Despite this influence of interfragment habitat, our lack of relationships between canopy loss and species richness/presence suggests that habitat quality within fragments has not affected the species composition.

If further exploration reveals that baboons are resident in Ibiki and red colobus are resident in Kiranzi-Kitungulu, the repeated GLM analysis for uncertain fragments suggests that AMI range and isolation by farmland should be considered weaker predictors of resident species richness ($P = 0.011$ and 0.024). However, given that Ibiki is a narrow forest adjacent to a large area of farmland, and that baboons are opportunist crop-raiders, it is very likely that they are transitory rather than resident. Furthermore, if red colobus remain in Kiranzi-Kitungulu, their population is unlikely to be viable.

Red colobus may have been exterminated by hunting in the Udzungwa highlands [Rodgers et al., 1980]. Indeed most species of red colobus are vulnerable to hunting [Struhsaker, 1999, 2005]. Hunting may explain why no monkeys were resident in the small forest of Itanga, given their presence in three smaller isolated fragments (Table I). The heavily hunted Kisinga-Rugaro forest also appears

as an outlier (Fig. 2), where red colobus were once present [Lovett & Pocs, 1993]. Repeated weak and near-significant relationships with species richness and red colobus presence ($0.0078 \leq P \leq 0.068$), and our analysis of isolated and hunted upland forest fragments suggests that hunting may have had a local effect. However, the lack of relationships between hunting and species richness at the 95% level and confounding correlation between hunting and climate variables ($r \geq 0.72$) suggest that it has not driven the SAR.

Like species richness, the presence of black and white colobus and of Sykes' monkeys was most related to forest area (Table III). There was little association with other human and climate variables, perhaps because of flexible diets and adaptability to habitat change [Marshall, 2007; Rovero et al., 2009]. Red colobus exhibit a stronger relationship with climatic variables (Table III). Red colobus also have the most restricted range of the four species tested for presence/absence, and previous studies of relative density, group size and composition suggest that they are more vulnerable to habitat disturbance [Rovero et al., 2009 and references therein]. The red colobus was the only species to exhibit a relationship with maximum dry-season precipitation (Table III), a good predictor of plant species' occurrence in the Eastern Arc Mountains [Platts et al., 2008]. Presumably the common monkeys are more adaptable to dry conditions due to greater dietary flexibility than the red colobus and greater mobility than plants.

For red colobus the observed relationship with climate, and a previously observed relationship between abundance and elevation [Marshall et al., 2005], may explain their absence from seven of the ten small high elevation forests ($<12 \, \text{km}^2$; Table I). However, red colobus persist in three high elevation forests that are neither hunted nor isolated by farmland (Table I). In addition, where hunting and isolation are absent, the three most common species (Sykes' monkey, red colobus and black and white colobus) are found across the elevation range.

The two rare papionins (Sanje mangabey and kipunji) are found only in the three largest forests, but no forest contains both species (Table I). Primates that have a highly frugivorous diet typically require large habitat patches [Marsh, 2003]. Despite a lack of geographic overlap, an elevation overlap suggests spatial partitioning (Sanje mangabey 300–2,080 m [Ehardt et al., 2005]; kipunji 1,300–1,800 m in Ndundulu, 1,250–2,790 m in the Southern Highlands [southwestern Tanzania; Davenport et al., 2008]). The limited range of kipunji and other monkeys in Udzungwa could also be explained by unknown influences such as biogeography or historic hunting.

The yellow baboon presence was predicted by the warm, wet climate of low elevation forests, but not by any variables relating to human influence (Table III). This influence is evident in the species

richness analyses incorporating transitory species (predominantly baboons), where the relative strength of climate variables over human variables was higher than for resident species. The lack of relationship between yellow baboons and human factors extends the trend in reduced vulnerability to disturbance with increasing extent of occurrence, as seen for the forest monkeys above. Baboons are present in farmland at all elevations, but not in high elevation forest (Table I). The low productivity of high elevation forests provides few resources for such animals, whose ecology is constrained by the availability of fruit and invertebrates [Wahungu, 1998].

Previous studies have paid little attention to residency, which may be particularly important in Africa, where several primate species are found outside of forest habitats. Because of the difficulty in determining the presence of transitory species, we are cautious about drawing firm conclusions regarding these species. Animals that occur inside small forests but rely on external resources have an ''effective patch size'' greater than the forest area alone [Andrén, 1994]. Our caution in the use of transitory species is supported further by the reduced relationships observed between species richness and forest area, isolation by farmland and AMI range, when incorporating transitory species.

Overall the observed significant results can be summarized using niche theory. A species' fundamental niche is that defined by the theoretical limits of species presence [Chase & Leibold, 2003]. While climate determines a species' fundamental niche, humans have a strong influence on the realized niche, as seen from the strong statistical relationships between resident species richness and both area and isolation. The Udzungwa red colobus is affected by the disturbance at high elevations, where the species is potentially more vulnerable to human influences because they are at the limit of their climatic niche space and productivity is low. There may also be some unmeasured influences that correlate with isolation and fragment size, such as the prevalence of parasites, which increased with fragmentation and human disturbance in a Ugandan forest meta-population [Gillespie & Chapman, 2006; Gillespie et al., 2005].

Implications for Conservation Management

The log-linear relationship suggests that conservation management to assist growth of small forests to at least $150 \, \text{km}^2$ would encourage a species-rich primate community (Fig. 2B). Management based on species richness may conserve biodiversity, as areas with high species richness can coincide with taxonomically important species [Hacker et al., 1998]. However, the presence of a species does not indicate population health or habitat quality and reserve design requires consideration of several

factors beyond species richness [McCarthy et al., 2006; Orme et al., 2005; Struhsaker, 1981]. Our analyses further show the importance of management for increased habitat heterogeneity by safeguarding forests across the elevation gradient. In particular, farming is most likely to develop in lowland areas of high productivity, resulting in habitat loss and increasing human populations. Prevention of widespread grassland fires would also encourage connectivity between otherwise isolated fragments [Marshall et al., 2001], potentially increasing dispersal and the viability of restricted-range species.

ACKNOWLEDGMENTS

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