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Research

A standardized assessment of forest mammal communities reveals consistent functional composition and vulnerability across the tropics

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The understanding of global diversity patterns has benefitted from a focus on functional traits and how they relate to variation in environmental conditions among assemblages. Distant communities in similar environments often share characteristics, and for tropical forest mammals, this functional trait convergence has been demonstrated at coarse scales (110–200 km resolution), but less is known about how these patterns manifest at fine scales, where local processes (e.g. habitat features and anthropogenic activities) and biotic interactions occur. Here, we used standardized camera trapping data and a novel analytical method that accounts for imperfect detection to assess how the functional composition of terrestrial mammal communities for two traits – trophic guild and body mass – varies across 16 protected areas in tropical forests and three continents, in relation to the extent of protected habitat and anthropogenic pressures. We found that despite their taxonomic differences, communities generally have a consistent trophic guild composition, and respond similarly to these factors. Insectivores were found to be sensitive to the size of protected habitat and surrounding human population density. Body mass distribution varied little among communities both in terms of central tendency and spread, and interestingly, community average body mass declined with proximity to human settlements. Results indicate predicted trait convergence among assemblages at the coarse scale reflects consistent functional composition among communities at the local scale, suggesting that broadly similar habitats and selective pressures shaped communities with similar trophic strategies and responses to drivers of change. These similarities provide a foundation for assessing assemblages under anthropogenic threats and sharing conservation measures.

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Introduction

In an epoch of unprecedented biodiversity loss, understanding diversity patterns and the vulnerability of species and communities to anthropogenic threats is increasingly relevant to conservation. Studies of global diversity patterns have emphasized the comparison of species richness (Gotelli and Colwell 2001, Roll et al. 2015, Torres-Romero and Olalla-Tárraga 2015) and turnover (i.e. taxonomic and phylogenetic beta diversity) (Buckley and Jetz 2008, Melo et al. 2009), though there is increasing interest in trait-based evaluations (McGill et al. 2006, Petchey and Gaston 2006, Safi et al. 2011, Kissling et al. 2012). ‘Functional traits’ are characteristics that reflect niches and life history strategies (McGill et al. 2006), and their distribution can be compared among assemblages and related to environmental conditions regardless of taxonomy and evolutionary history. Functional traits have been extensively used in studies on plants (Poorter and Bongers 2006, Kunstler et al. 2015), and recently also on vertebrates such as birds (Kissling et al. 2012), but relatively less on mammals (but see Safi et al. 2011, Vetter et al. 2011). This is unfortunate, as mammals not only include many of the most charismatic and threatened animals on earth, they also fulfil a variety of important ecosystem functions, ranging from seed dispersal and seed predation to herbivore control, nutrient cycling and habitat engineering, which in turn have direct and indirect effects on plant community dynamics and ecosystem services (Jansen et al. 2010, Osuri et al. 2016).

Broad-scale analyses based on predicted species distributions suggest that mammal communities occurring in similar environments exhibit similar patterns in functional traits irrespective of differences in taxonomy and evolutionary contexts (Penone et al. 2016, Mazel et al. 2017). These patterns have been attributed to the upscaling from species to assemblages of convergent evolution to exploit analogous opportunities (i.e. niches) in independent lineages under similar environmental constraints (Reich et al. 1997, Samuels and Drake 1997, Muschick et al. 2012). Penone et al. (2016), in particular, used habitat suitability models to predict mammalian species distributions and compare assemblages across the tropical forest biome, and found similar ‘functional trait composition’ (Lawing et al. 2017; hereafter ‘functional composition’) even among taxonomically distinct communities and isolated environments. These authors used body mass and correlated morphological and reproductive measures as functional traits, and suggested that in view of broad habitat similarities within tropical forests, distantly related mammal lineages have evolved to exploit forest habitats in similar ways (Ricklefs 2010, Jetz and Fine 2012). However, empirical tests of these predictions are lacking, largely due to a lack of systematic field studies collected at fine spatial scales; analyses using coarse scale data (assemblages defined at 110 to 200 km

resolution) could not determine whether the pattern of functionally-convergent assemblages also occurs at the local scale that applies to distinct communities. Yet, analyses conducted on range map data and survey data can generate different results and the discrepancy may have important implications in ecology and conservation (Hurlbert and White 2005).

Multiple factors may influence the diversity of functional compositions among communities at the local scale. First, anthropogenic pressures, with habitat fragmentation and land use change as primary drivers (Crooks et al. 2017), are causing unprecedented extinctions of land mammals (Shipper et al. 2008). Evidence from vertebrates suggests that these threats lead to the extinction of species that are larger, have more specialized niches, and have a high functional importance (Pimm et al. 1988, Purvis et al. 2000), resulting in a skewed community structure (Petchey and Gaston 2002, Duffy 2003). In particular, studies on birds across the tropics revealed that land use changes affect disproportionately particular trophic guilds (i.e. insectivores and frugivores; Newbold et al. 2013, 2014), potentially altering the ‘trophic guild composition’ of communities, i.e. the relative richness of trophic guilds (Kissling et al. 2012). Similarly, studies on mammal and bird assemblages suggest that average body mass is lower in disturbed and/or fragmented habitats versus undisturbed habitats (Lomolino and Perault 2007, Bregman et al. 2014). Second, local processes associated with climate, habitat and lineage history may affect the diversity of functional compositions among communities within supposedly homogeneous habitats. For example, Kelt et al. (1996) studied small mammal communities in the world’s deserts and found similarities in functional composition across regions but also important differences, especially in the representation of specialized trophic guilds such as the granivores and carnivores. Beaudrot et al. (2016a) found that trait diversity of ground dwelling mammals and birds from 14 of the 16 forests in our study was lower for communities in Africa than in other continents. Third, anatomical, physiological or behavioural traits that have been previously overlooked, for example those underlying the convergent evolution of herbivory in kangaroos and deer, could explain niche similarities among morphologically different species when selective pressure for a particular strategy does not require morphological adaptation (Mazel et al. 2017). Thus, similar habitats within the tropics may select for species with similar body masses and related life history traits but varying trophic strategies, potentially leading to variation in the trophic guild composition of their communities. The use of trophic guild (i.e. diet) as a key functional trait is a promising approach to assess niche-related similarities in functional composition, as indicated by a number of studies (Safi et al. 2011, Mazel et al. 2017).

As functional traits indicate both how organisms respond to changes (‘response traits’, e.g. body mass) and how they contribute to ecosystem function (‘effect traits’, e.g. trophic guild) (Díaz et al. 2013, Hevia et al. 2017), understanding whether the predicted similarities in functional traits among mammal assemblages are maintained at the scale of local

communities is relevant to assess their vulnerability and how ecosystem function may be altered (Thornton et al. 2011, Vetter et al. 2011, Kissling et al. 2012, Newbold et al. 2014). In turn, understanding functional responses of mammal communities to biotic and abiotic environmental changes can be used to better define conservation and management strategies for the long-term viability of these important communities, including defining protected areas (Laurance et al. 2012), buffer zones (DeFries et al. 2010) and planning habitat- or species-level restoration efforts (Duffy 2003).

The detailed knowledge of mammalian functional traits available relative to other organisms offers an excellent premise to study the functional composition of communities. However, there remain practical difficulties of conducting studies across multiple communities in a systematic way that can produce data sufficient to investigate drivers of geographic variation in community characteristics. Moreover, observed or predicted species occurrences and abundances may be biased due to imperfect detection, which makes the estimation of true community size and composition difficult from error prone observational studies (Dorazio et al. 2006, Thornton et al. 2011). Imperfect detection also results in partial representations of species within a community, with rare species being under-represented and common species being over-represented (Si et al. 2018). A possible solution to this problem comes from standardized surveys using camera traps, i.e. motion-sensitive cameras that photograph passing animals. Camera trapping also suffers detection bias, but this can be addressed by hierarchical models that formally incorporate the detection process (Royle and Dorazio 2008). This unbiased approach can be adapted to integrate and compare data across multiple sites and regions (Sutherland et al. 2016).

Here, we assess how the functional composition of communities of ground-dwelling medium to large terrestrial mammals in tropical forests varies in relation to habitat characteristics and anthropogenic pressures. We used standardized camera trapping data from 16 mammal communities collected by the Tropical Ecology, Assessment and Monitoring (TEAM) Network (Rovero and Ahumada 2017) in three continents. Communities are in closed-canopy forests within protected areas, despite variable fragmentation and size of surrounding human populations in their landscape. We assess trophic guild and body mass as the functional traits of interest, as they determine resource and niche requirements (Safi et al. 2011, Hevia et al. 2017, Mazel et al. 2017). We used a hierarchical multi-region community model, a novel analytical framework for quantifying geographic variation in species richness and composition of communities in four trophic guilds (carnivores, herbivores, omnivores and insectivores) while accounting for imperfect detection by camera traps (Sutherland et al. 2016, Tenan et al. 2017). We asked if the broad-scale similarities in functional trait composition among assemblages are maintained at local scales. We address three hypotheses: 1) broad similarities in habitat type and protection among forests result in communities with consistent trophic guild compositions and body mass distributions; 2) the functional composition

varies among communities, but similar pressures (i.e. habitat characteristics and/or human activities) result in consistent changes in trophic guilds and body mass distributions. In particular, we expect carnivore and insectivore richness to be positively associated with protected habitat size and/or negatively with anthropogenic pressure, and average community body mass to be negatively associated with anthropogenic pressure (Purvis et al. 2000, Newbold et al. 2014). 3) Communities in different regions differ idiosyncratically.

Material and methods

Camera trap data

Data came from 16 areas in tropical moist forest that form the TEAM Network (Supplementary material Appendix 1 A1 Methods, Table A1). TEAM monitors ground-dwelling tropical mammal and bird communities using camera trap arrays (TEAM Network 2011). In each area, these consist of 60 camera trap points (camera trap model RM45, HC500, PC900, Reconyx) deployed at a density of one camera per 2 km² for at least 30 consecutive days during the dry season (months with less than 100 mm average rainfall). The density was reduced to one camera per 1 km² at two sites (Volcan Barva and Pasoh) as the overall forest area was not large enough. We considered the area effectively sampled by camera traps (minimum of 120 km² for most sites) to represent an adequate scale to study communities of medium to large mammals, ensuring inclusion of the largest species whose home ranges may be in the order of hundreds km² (TEAM Network 2011). Arrays are regular grids of camera traps set close to animal trails and without bait to avoid biasing detections. Two or three arrays of 20–30 camera traps were deployed sequentially rather than simultaneously. Arrays sampled the most dominant habitat type within the site and were distributed along altitudinal gradients if they were present. All data used for this study were collected in 2011 except at the Caxiuaná TEAM site, where we used data collected in 2010. A single taxonomic authority was used for naming mammal species (IUCN 2016). All TEAM data are publicly available at <<http://www.teamnetwork.org>>.

The realized sampling effort was 27 660 camera days from 922 camera traps that effectively operated (range 50–60 per site). We obtained 300 257 images of predominantly terrestrial, medium to large mammals (range 1215–74 723 per community). We included in the analysis 171 species of mammals for which 1) body mass (sourced in Smith et al. 2003) was greater than or equal to 75 g (smaller species being of difficult detection and/or identification) and 2) data (IUCN 2016; Animal Diversity Web; <<http://animaldiversity.org/>>) indicated the species spends a large proportion of its time on or near the ground. These species were detected through 15 003 (range 188–2567 per community) daily detection events. The list of species with relevant metadata is in Supplementary material Appendix 1 Table A2.

Species traits and covariates

As species' traits we used 1) species-level body mass (g) and 2) trophic guild. Body mass ranged from 75g to 3940kg, with a median of 3910g. In the analysis we considered body mass on the log scale, to account for the markedly skewed distribution. Each species was categorized as one of four trophic guilds: carnivore (35 species), herbivore (79), insectivore (20), or omnivore (37). We sourced the EltonTraits database (Wilman et al. 2014) for diet composition data and used the criteria in Robinson and Redford (1986) and Fa and Purvis (1997) to assign categories. Thus, we classified as herbivores species feeding on $\geq 50\%$ on plant material, as carnivores species feeding on $\geq 50\%$ on vertebrates, as insectivores species feeding on $\geq 50\%$ on invertebrates, and the rest as omnivores, i.e. species feeding on both plant and animal material, including the omnivore-frugivores (species feeding on $\geq 50\%$ on fruits and the rest on animal material). The two functional traits we considered are fundamental descriptors of species' niche. Body mass is correlated with many other fundamental life history traits including adult body size, life span and litter size (Millar and Zammuto 1983), hence diet and body mass are widely applied to defining the mammal communities (Ahumada et al. 2011, Safi et al. 2011, Mazel et al. 2017). Moreover, because our focus was ground-dwelling mammals, we did not include 'habit' or foraging stratum (e.g. aquatic, fossorial, arboreal, etc.).

To model variation in guild richness we used the following set of 12 environmental and human disturbance covariates. We drew them from a broader set of candidate covariates based on avoiding collinearity (using correlation coefficient of $r=0.5$ as the reference threshold) and ecological relevance (Supplementary material Appendix 1 Table A1; see A1 Methods for covariate details). We considered the first six variables as predictors of habitat diversity and quality: 1) elevation range of camera traps, a proxy of terrain morphology and habitat heterogeneity. 2) Normalized difference vegetation index (NDVI), an indicator of green vegetation biomass (Pettorelli et al. 2005), and hence of habitat characteristics. 3) Tree mean basal area, from 1-ha vegetation at TEAM forests, a proxy of forest age and stability. 4) Tree stem density, a proxy of forest structure; we also used 5) squared stem density to account for potential mid-range peaks in values. 6) Mean annual precipitation. We also considered the following six variables, as predictors of potential anthropogenic pressure: 7) averaged distance of camera traps to settlements, a proxy of human disturbance. 8) Extent of protected area where TEAM site is inscribed, a proxy of protected habitat area. 9) Mean edge density of forest classes (standardized edge per unit area), a proxy of habitat fragmentation. 10) Illegal hunting score, a proxy of the intensity of poaching. 11) Spatial extent of the zone of interaction (ZOI). Since processes outside of the reserve may affect mammals inside the reserve, we examined the broader landscapes; the ZOI estimates this area based on systematic quantification of contiguous habitat areas and surrounding watersheds, migration corridors and areas with human activities (DeFries et al. 2010). 12) Human population density within the ZOI.

Model formulation

We modelled variation in community functional composition among forests using the 'multi-region community model' described by Tenan et al. (2017). We compared community composition of $R=16$ communities based on $G=4$ trophic guilds (carnivore, herbivore, insectivore, omnivore) and body mass. We assumed that each species $i=1,2,\dots,n_r$ (with n_r ranging from 16 to 29, median 22) in region r can be assigned to only one feeding guild, with membership denoted by the guild indicator variable $\mathbf{g}_{i,r}$. 'Region' is defined following Sutherland et al. (2016), i.e. a single spatial unit or community of interest with a unique species composition that is independent of other regions. Thus, we modelled the geographic variation in region- and guild-specific richness (N_{gr}) as a Poisson random variable, $N_{gr} \sim \text{Poisson}(\lambda_{gr})$, where λ_{gr} is the expected richness modelled as a function of the 12 region-specific covariates listed above (\mathbf{cov}_r) and additional random variation ($\epsilon_{\lambda,gr}$):

$$\log(\lambda_{gr}) = \beta_{0g} + \beta_{\text{cov},g} \text{cov}_g + \epsilon_{\lambda,gr}, \text{ with } \epsilon_{\lambda,gr} \sim N(0, \sigma_\lambda^2) \quad (1)$$

Following Tenan et al. (2017) we derived the proportion of all species belonging to each guild as the probability that species i , in region r , belongs to guild g , i.e. $\pi_{gr} = \lambda_{gr} / \sum_g \lambda_{gr}$. This proportion quantifies the trophic guild composition^g (see Introduction). We assessed the strength of evidence, or degree of support, for each covariate in the linear predictors for guild species richness by calculating the posterior variable inclusion probability ($\Pr(w_{\lambda,\text{cov},g}) = 1$), i.e. the probability that a variable is 'in' the model, using the Gibbs variable selection approach (GVS) (Tenan et al. 2014). Here we apply GVS for 12 explanatory variables, and while this would typically be considered overfitting for only 16 regions, GVS has been shown to be a reliable approach for variable selection even in cases when the number of explanatory variables is much larger than sample size (Wenxin 2007). For further details on the variable selection procedure, see Supplementary material Appendix 1 A1 Methods.

The functional group membership variable was modelled as $\mathbf{g}_{i,r} \sim \text{Cat}(\boldsymbol{\pi}_r)$, with $\boldsymbol{\pi}_r$ elements of g -length vector $\boldsymbol{\pi}_r$. We considered species body mass ('mass') as a covariate on detection probability (Supplementary material Appendix 1 A1 Methods for model formulation details). This allowed us to estimate the expected body mass distribution for all species in each community. In addition, region-specific mean body mass $\mu_{\delta_{\text{mass},r}}$ was modelled as a function of 1) illegal hunting score, 2) distance to settlements, 3) extent of protected area, 4) human population density within the ZOI and 5) spatial extent of the ZOI:

$$\mu_{\delta_{\text{mass},r}} = \zeta_0 + w_{\text{mass,cov}} \zeta_{\text{cov}} \text{cov}_r \quad (2)$$

where ζ_{cov} is the slope for the effect of each covariate ('cov') on the region-specific body mass. As with guild richness and probability, we estimated posterior variable inclusion

probabilities, $\Pr(w_{\text{mass, cov}}) = 1$, and retained the predictors for which $w_{\text{mass}} > 0.5$.

The matrix of true occupancy states \mathbf{Z} is a 3-dimensional array containing the species-by-site-by-region occupancy states z_{ijr} , with site $j = 1, \dots, J_r$ (with J_r ranging from 50 to 60, median 59). Site- and region-specific occupancy states are described as $z_{ijr} \sim \text{Bern}(\Psi_{ijr}, \omega_{ir})$, where Ψ_{ijr} is the species-specific occurrence probability for each site in each region and ω_{ir} is the parameter denoting whether species i was present in the r^{th} community ($\omega_{ir} = 1$) or whether it is a structural zero ($\omega_{ir} = 0$). For species that were observed in a region, $\omega_{ir} = 1$ is fixed. Note that, in the model formulation, $\omega_{ir} \sim \text{Bern}(\Omega_r)$, where Ω_r is the proportion of $M - n_r$ ‘all-zero’ encounter histories representing undetected species members of the r^{th} community (i.e. sampling zeros and not structural zeros). Note that Ω_r and N_r are equivalent parameters, since $E[N_r] = \Omega_r M$. By conditioning on the total community size, Ω_r is thus confounded with $\exp(\beta_0)$ and one of the two parameters has to be fixed. We thus specified $\Omega_r = \sum_g \lambda_{gr} / M$. Model formulation details for occupancy and detection probability are reported in Supplementary material Appendix 1 A1 Methods.

Encounter frequency data were organized as a 3-dimensional $n_{\text{max}} \times J_{\text{max}} \times R$ detection – non-detection matrix \mathbf{Y} , with matrix elements y_{ijr} . Maximum number of observed species in a community was n_{max} and maximum number of camera trap sites sampled in a community J_{max} . We modelled observed detection frequencies as $y_{ijr} \sim \text{Bin}(K_{jr}, p_{ijr}, z_{ijr})$, with detectability (p) as a function of distance to roads and body mass (Supplementary material Appendix 1 A1 Methods for more details). We fitted models using a Bayesian formulation, the

Markov chain Monte Carlo framework, and the data augmentation technique (Royle et al. 2007, Royle and Dorazio 2008; see Supplementary material Appendix 1 A1 Methods for more details and Script A1 for the model code).

Results

We found that the 16 communities share a similar composition in trophic guilds, with no significant variation in the estimated proportions of trophic guild richness, i.e. 95% Bayesian credible intervals overlapped (Fig. 1; Supplementary material Appendix 1 Table A3). To determine how our communities were influenced by anthropogenic pressure, habitat characteristics and scale of protection we examined 12 potential predictors of trophic guild richness (see Methods and Supplementary material Appendix 1 Table A4; results of observed and estimated guild and community richness are reported in Supplementary material Appendix 1 A1 Methods and Table A5, A6). The best model included three of these predictors, namely 1) the normalized difference vegetation index (NDVI), a measure of green vegetation biomass, 2) reserve size (the extent of protected area) and 3) human density in the zone of interaction (ZOI, i.e. the extent of the broader landscape encompassing the protected area where threats to communities are considered most intense) (Supplementary material Appendix 1 Table A4). These variables spanned a wide range: NDVI from 0.06 to 0.65, reserve size from 136 to 17 000 km² and human population density in the ZOI from 0.06 to 358 km⁻² (Supplementary material Appendix 1 Table A1). The model detected significant

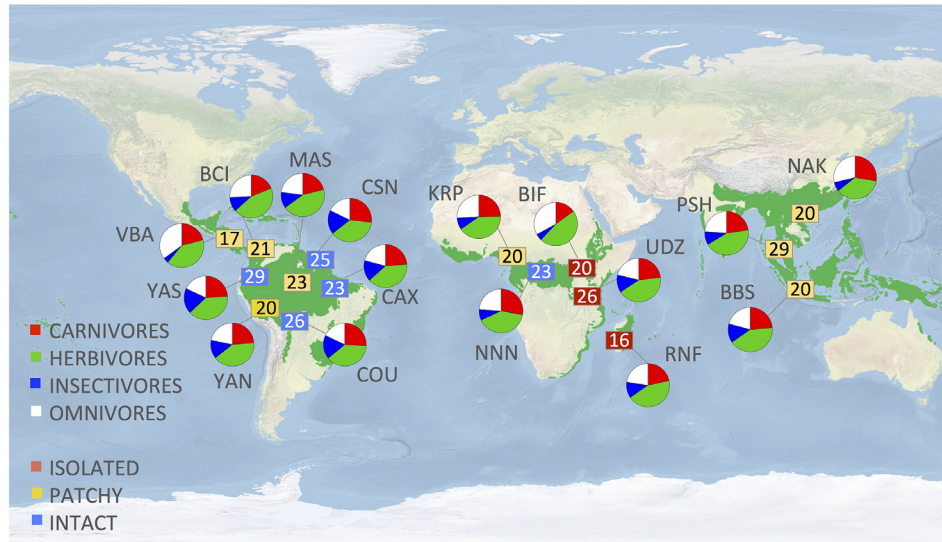


Figure 1. The 16 tropical forest protected areas in the TEAM Network where mammal communities were assessed with standardized surveys using camera traps. For each community, pie charts report the trophic guild composition as the mean estimates of the proportion of species in each trophic guild on the total species richness. These proportions, for each guild, did not significantly vary among communities across the tropics (see also Supplementary material Appendix 1 Fig. A1). The numbers in the coloured squares are the observed species richness and the colours indicate the type of landscape according to fragmentation level (see legend). Full names of study areas and other details are in Supplementary material Appendix 1 Table A1. Green shading depicts tropical forest.

(i.e. probability of a negative or positive effect $p[\theta > 0] \geq 0.95$), or marginally significant relationships only for insectivore richness, which increased with reserve size ($p[\theta > 0] = 0.98$, mean effect = 0.427) and NDVI (0.94, mean effect = 1.919) and decreased with the human population density in the ZOI ($p[\theta > 0] = 0.94$, mean effect = -0.368; Fig. 2; Supplementary material Appendix 1 Table A7). This indicates greater sensitivity by insectivores to primary productivity and protected area size, and to anthropogenic pressure, while the richness of the other trophic guilds did not appear to be significantly sensitive to these factors. The relationships of guild richness with predictors were reflected in similar gradients in trophic guild composition. In particular, the proportion of insectivores decreased with increasing human density in the ZOI and increased with reserve size (Supplementary material Appendix 1 Fig. A1, Table A3).

The median (SD) body mass of the species detected in each community ranged from 0.88 (12.02) kg in Ranomafana to 13.90 (816.26) kg in Noubalé Ndoki. Much of this variation was driven by the presence or absence of elephants, found in only five of the 16 communities. Nonetheless, community body mass distributions, which include unobserved

species, were broadly consistent, both in terms of their central tendency (Supplementary material Appendix 1 Table A8) and spread (Supplementary material Appendix 1 Fig. A2). Interestingly, average body mass was positively and significantly associated with distance to human settlements ($p[\theta > 0] = 1$, mean effect = 0.162; Fig. 3 and Supplementary material Appendix 1 Table A9, A10). Results on patterns of average occupancy and detectability estimated for each community are reported in Supplementary material Appendix 1 A1 Results, Table A11–A16.

Discussion

We found that the trophic guild composition of the 16 forest mammal communities was remarkably consistent and responded similarly to protected habitat size and characteristics, and to anthropogenic pressure, with insectivores being the most sensitive guild. Body mass distributions were also consistent, and average community mass was negatively related to proximity to human settlements. The consistency in functional composition and sensitivity to changes among

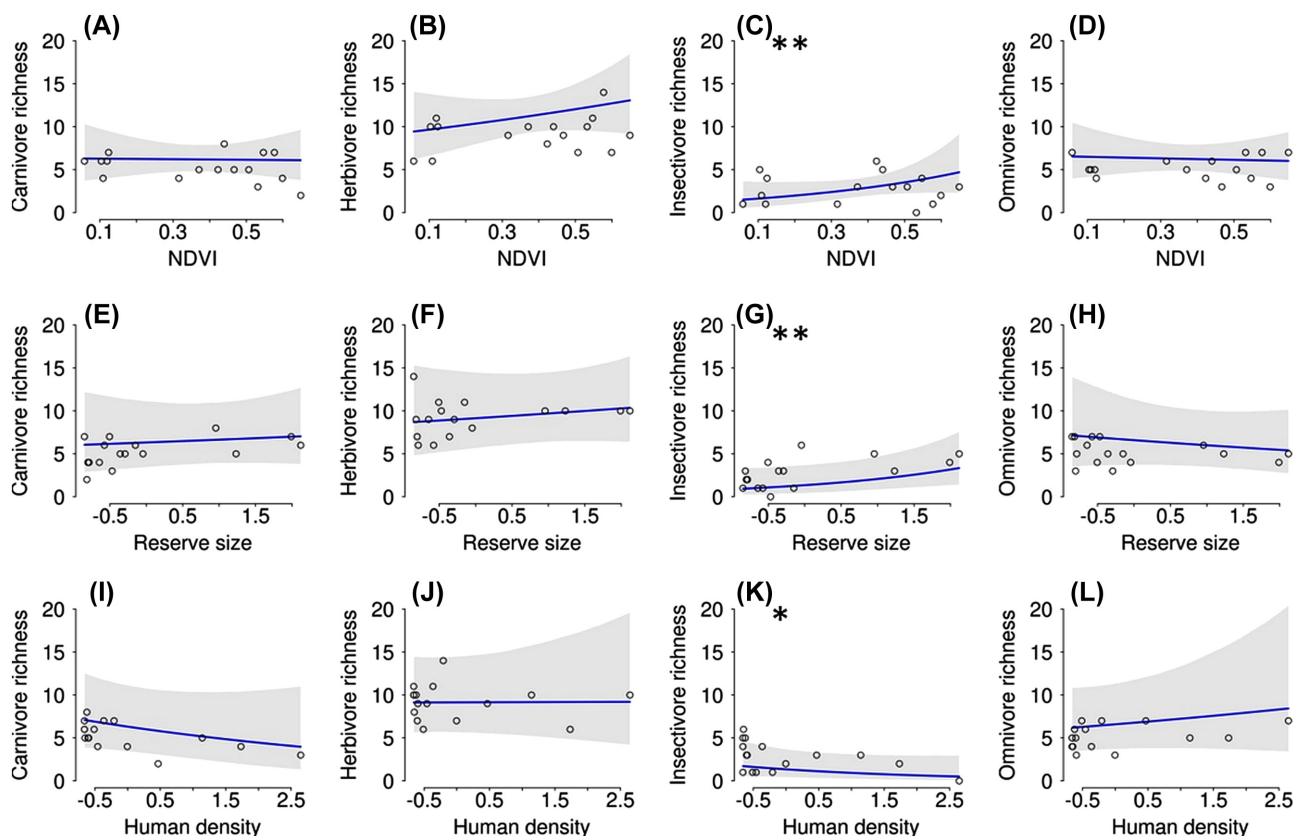


Figure 2. Relationships between estimated species richness of four trophic guilds (carnivores, herbivores, insectivores and omnivores) in tropical forest mammal communities and three potential predictors of variation, namely normalized difference vegetation index (NDVI; panels A–D), reserve size (E–H) and human population density in the zone of interaction (ZOI; I–L). Grey areas indicate 95% Bayesian credible intervals. Open circles indicate observed guild richness of the 16 communities. All covariates are standardized except for NDVI. Reserve size and NDVI had a significant effect on the estimated richness of insectivores (panels C–G, respectively, marked by two asterisks), while human density in the ZOI had a marginally significant effect (panel K, one asterisk; Supplementary material Appendix 1 Table A7).

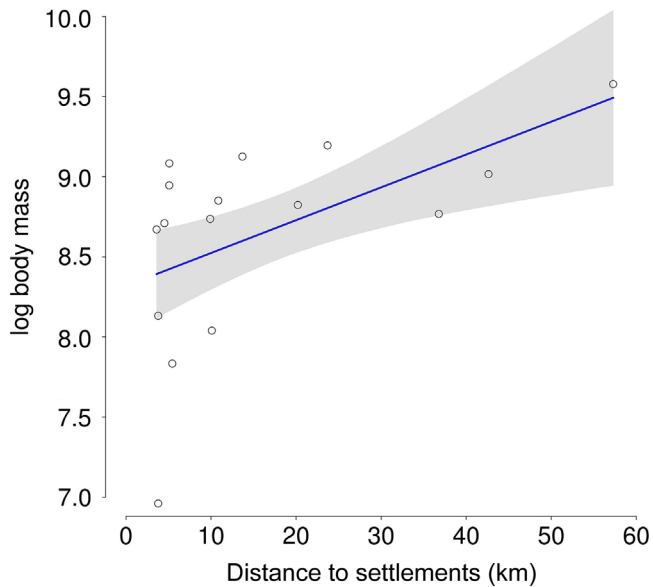


Figure 3. Relationship between region-specific mean body mass and distance to settlements. Grey areas indicate 95% Bayesian credible intervals. Open circles indicate mean body mass for the observed species of the 16 communities.

communities occurred despite the taxonomic differences and the considerable variation in habitat and in anthropogenic pressures.

Our findings validate the similarity of tropical forest mammal communities suggested by a previous broader-scale study (Penone et al. 2016). Our observations also support the hypothesis that habitat characteristics and anthropogenic pressure induce similar functional responses in these communities. Trait similarity among distinct communities is consistent with convergent evolution (Samuels and Drake 1997, Mazel et al. 2017). This is also consistent with both experimental (Fukami et al. 2005) and empirical results for plants and other organisms (Reich et al. 1997, Gillespie 2004, Muschick et al. 2012). Thus, in view of the age and stability of tropical broadleaf forests, and broad similarities in climate and day length, mammals from distant regions would have converged to exploit forest habitats in similar ways (Ricklefs 2010, Jetz and Fine 2012). The communities that we studied included examples of functional similarities among taxonomically-distant taxa in all guilds. For example, among the insectivores, the armadillo of Nouabalé Ndoki, Republic of Congo, is comparable to anteaters in the Neotropical communities. While belonging to different orders, armadillo and anteaters share powerful digging forearms, long tongues and toothless, tube-like snouts to feed on termite mounds. Among the omnivores, the civets and mongooses in Asian and African communities are functionally similar to procyonids such as the coatis in Neotropical communities. These species belong to different families in the Carnivora but all have short limbs, long tails, elongated snouts and are agile opportunistic omnivores.

Despite these morphological similarities among species, the predicted convergence in life history traits across assemblages at coarse resolution may not scale to similarities in the functional composition of communities, as local environmental factors and anthropogenic pressures may differentiate communities idiosyncratically (see Introduction). In small desert mammals, for example, both predictive (Penone et al. 2016) and empirical (Kelt et al. 1996) studies found remarkable differences across regions despite broad environmental similarities. These differences were attributed to the marked heterogeneity in local habitat and climatic conditions across deserts at different latitudes (Kelt et al. 1996, 1999, see also Read et al. 2018). Such heterogeneity is likely higher than within tropical moist forests that span a narrower latitudinal range and represent a relatively more stable biome (Jetz and Fine 2012). Moreover, by using trophic guild as a trait we could directly infer resource acquisition strategies as shared responses to similar niches (Hevia et al. 2017, Mazel et al. 2017), thus testing the hypothesis that the similarities in body mass and related life history traits do not correspond to similarities in trophic strategies (Penone et al. 2016 and Introduction). Our model was not designed to test for differences in guild richness among continents; however, results in Beaudrot et al. (2016a) of lower trait diversity of communities in Africa relative to other continents are not directly comparable with our results, as these authors used a functional dispersion index based on a variety of traits while we used the distribution of selected traits. While our results indicate that functional composition is consistent among communities regardless of taxonomic differences, how unmeasured region- or continent-specific characteristics influence this comparison remains to be assessed. We found that the estimated species richness of insectivores was positively related to NDVI and protected area size and negatively to human population density in the zone of interaction. Studies on vertebrates, mainly on birds, generally show greater sensitivity of insectivores to habitat size, quality and fragmentation relative to other guilds, possibly a result of large spatial requirements, dependence on old-growth forest and altered conditions potentially resulting in lower insect abundances along the edges (Stratford and Stouffer 1999, Vetter et al. 2011, Bregman et al. 2014). While evidence regarding mammals remains scant (but see Ahumada et al. 2011 and below), an analysis of tropical forest birds found that insectivores had a lower presence and abundance in areas most affected by anthropogenic disturbance and where forest cover was lost or degraded, conditions that were especially common at forest edges (Newbold et al. 2013). The consistent body mass distributions we reported among communities match patterns from wide-range assessments of mammalian body mass across similar habitats (Brown and Nicoletto 1991, Bakker and Kelt 2000). We also found that average body mass of communities increased with distance from human settlements. This variable correlates with distance to roads and reserve boundaries, and is a general measure of proximity to anthropogenic activities and disturbance (DeFries et al. 2010). Larger species

tend to have lower population densities, slower life histories and larger home ranges, and are known to be more vulnerable to a wider range of human activities (Pimm et al. 1988, Purvis et al. 2000).

Ahumada et al. (2011) previously assessed the size and functional composition of seven tropical forest mammal communities in the TEAM Network, and found that communities from fragmented forests tended to have lower species richness and higher dominance. This analysis is not directly comparable with ours as authors considered only species that were actually detected, and plotted the point estimates post-hoc instead of modelling them. However, while we found much less variation in species richness and functional composition than did Ahumada et al. (2011), our result of greater sensitivity of insectivores to anthropogenic pressure is in line with their finding that in more fragmented areas lower species richness appears related to an impoverishment in insectivores rather than other guilds. The different outcome between studies highlights the fundamental importance of modelling covariates with the associated uncertainty in such assessments (Link 1999, Sutherland et al. 2016). These novel methods (Tenan et al. 2017) ensure that estimates of species richness and functional composition account for species that may not be observed during the survey, which is especially important when comparing communities (Thornton et al. 2011, Hegerl et al. 2015). The value of this approach is clear for communities where complementary data on occurring species are available. For example, while we detected 26 species in the Udzungwa Mountains, Tanzania, the model estimated that 30 are in fact present (Supplementary material Appendix 1 Table A5, A6), as confirmed by additional surveys (Rovero et al. 2014). We acknowledge that the limited number of regions in our study, and the inherently sparse number of species in medium-to-large mammalian guilds (especially insectivores), may raise concern over the power of detecting changes in species richness among communities. However, using simulations, Sutherland et al. (2016) show that 15 regions (with a minimum of 50 sites sampled per region) in a multi-region framework are sufficient for reliable inference on geographic variation in community size. Future studies should take advantage of the scaling up of camera trap networks (Steenweg et al. 2017) to assess how medium-to-large mammals perform for studying community structure relative to more species-rich faunal groups.

The relative uniformity in functional composition across communities extends the results of Beaudrot et al. (2016b), who used data from 15 of the 16 communities in our study, and found that species richness and community level occupancies of mammals and birds were stable over three to eight years for most communities. While this indicates that wildlife decline was not detected during their survey period, local extinctions in the last decades have been reported in the range of 1–3 species in at least five communities. These are among the most fragmented or isolated forests: Barro Colorado Island and Soberania National Park, Panama (white-lipped peccary, giant anteater and probably jaguar reported as locally extinct), Nam Kading, Laos (tiger and leopard), Bwindi, Uganda

(buffalo, leopard, giant forest hog) and Korup, Cameroon (leopard, golden cat, giant pangolin). High extinction rates of tropical forest mammals are typically caused by uncontrolled hunting and habitat loss (Dirzo et al. 2014, Hegerl et al. 2015), at intensity levels that are seemingly not occurring at TEAM forests during the time that they have been monitored (Beaudrot et al. 2016b). In the Udzungwa Mountains, for example, decades of uncontrolled hunting and degradation in a nearby forest have almost halved the number of species and changed the functional composition relative to the less disturbed study forest sampled by TEAM (Hegerl et al. 2015). We therefore caution against generalizing our results to unprotected forests. We also stress that the relatively unaltered functional composition of communities does not imply that their ecological function is complete, as this also depends on numerical representation, not just species occurrence. Finally, we note that modern mammal communities reflect not just recent, but also prehistoric extinctions of many species of megafauna (Stuart 2015). Thus current mammal communities may already reflect human impacts to a greater degree than is readily apparent, and the differences among them, at least in terms of the largest species, may reflect the past impact of human activities (Smith et al. 2018).

In conclusion, our results indicate that mammal communities within protected areas have a consistent functional composition across the tropical forest biome. We targeted communities in protected areas as anthropogenic impacts are typically less severe than outside such areas and the communities are likely to be more complete. Nonetheless, we found that trophic guild and body mass patterns can be associated with changes in anthropogenic pressure, and that particular guilds, namely the insectivores, are sensitive to the size of the protected area, characteristics of its habitat, and surrounding human population density. The conservation of mammal communities, including the most sensitive species, requires maintaining large continuous areas of well protected habitat within a broader landscape with limited anthropogenic pressure. Given the similarities in vulnerability by communities to anthropogenic changes, our findings also suggest that effective conservation strategies might be transferable across areas. Functional composition can be used as a proxy for the ‘integrity’ of communities, which is a relevant feature for conservation prioritization. For example, Key Biodiversity Areas, a widely used conservation priority framework, uses ‘Ecological Integrity’ as one of the criteria for their delineation (Langhammer et al. 2018).

Our analyses based on field data complement global prioritization analyses for land mammals based on habitat suitability models (Brum et al. 2017), as recommended by the global mammal conservation strategy (Rondinini et al. 2011). Thus, our results address an important gap in comparisons between range and survey data (Hurlbert and White 2005). For example, a recent study developed high resolution models of habitat fragmentation and how this impacts the world’s terrestrial mammals (Crooks et al. 2017). Results show that mammals occurring in habitats with more fragmentation are at greater risk of extinction, and can be used to assess how reserves with

varying size and fragmentation maintain species. Our work provides field data on species occurrences and vulnerabilities that Crooks et al. (2017) recommend for model validation. Our findings on the importance of reserve size and anthropogenic pressures provide valuable insights from real-world scenarios.

Data availability statement

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.rbzns7h6z>> (Rovero et al. 2019).

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Supplementary material (Appendix ECOG-04773 at <www.ecography.org/appendix/ecog-04773>). Appendix 1.