

## LETTER

# Global camera trap synthesis highlights the importance of protected areas in maintaining mammal diversity

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#### Abstract

The establishment of protected areas (PAs) is a central strategy for global biodiversity conservation. While the role of PAs in protecting habitat has been highlighted, their effectiveness at protecting mammal communities remains unclear. We analyzed a global dataset from over 8671 camera traps in 23 countries on four continents that detected 321 medium- to large-bodied mammal species. We found a strong positive correlation between mammal taxonomic diversity and the proportion of a surveyed area covered by PAs at a global scale ( $\beta = 0.39$ , 95% confidence interval [CI] = 0.19–0.60) and in Indomalaya ( $\beta = 0.69$ , 95% CI = 0.19–1.2), as well as between functional diversity and PA coverage in the Nearctic ( $\beta = 0.47$ , 95% CI = 0.09–0.85), after controlling for human disturbances and environmental variation. Functional diversity was only weakly (and insignificantly) correlated with PA coverage at the global scale ( $\beta = 0.22$ , 95% CI = –0.02–0.46), pointing to a need to better understand the functional response of mammal communities to protection. Our study provides important evidence of the global effectiveness of PAs in conserving terrestrial mammals and emphasizes the critical role of area-based conservation in a post-2020 biodiversity framework.

#### KEYWORDS

camera trap, functional diversity, human accessibility, human footprint, mammal diversity, protected area, species richness, taxonomic diversity

## 1 | INTRODUCTION

Humans are a dominant geographical and environmental force on the planet (Díaz et al., 2019). The current era has been termed the “Anthropocene” (Lewis & Maslin,

2015), with anthropogenic disturbances such as overexploitation, habitat destruction, and invasive species driving extensive loss of biodiversity and ecosystem services (Dirzo et al., 2014). The formal establishment of protected areas (PAs) is one of the most prominent conservation actions

for mitigating these losses. Globally, terrestrial protected area coverage has increased from 14.1% to 15.3% in the past decade (Maxwell et al., 2020), and this trend is expected to continue under international policy commitments to conservation. For example, the parties to the Convention on Biological Diversity (CBD) are expected to agree on a new global biodiversity framework with targets that may include protecting 30% of the planet by 2030 and 50% by 2050 (Dinerstein et al., 2019). Given the global focus on increasing PAs as a primary conservation strategy, it is critical to evaluate their effectiveness at conserving biodiversity (Bhola et al., 2020).

The effectiveness of PAs has been questioned because relatively few have sufficient management practices in place (Geldmann et al., 2015). While many PAs appear to be effective at protecting habitat, there is limited evidence about whether they also protected animal populations (Geldmann et al., 2013). For instance, declines in large mammals and other taxa have been documented in several PAs (e.g., Laurance et al., 2012), especially those that are inadequately funded (Waldron et al., 2017). Even within some relatively well-protected areas, wildlife habitats have been significantly degraded (Geldmann et al., 2019); wildlife can also be negatively affected by nonconsumptive activities such as recreation (Naidoo & Burton, 2020), and by human-altered fire activity (Mansuy et al., 2019).

In many respects, pressures on wildlife within PAs reflect the broader impacts of human activities across the planet (Geldmann et al., 2014; K. R. Jones et al., 2018; Wittemyer et al., 2008). The “human footprint” (hereafter footprint) is often used to characterize cumulative human disturbances across terrestrial landscapes, which now extend across 75% of the planet’s land surface and have been linked to changes in the behavior, distribution, and diversity of medium- and large-bodied mammals (Belote et al., 2020; Tucker et al., 2018; Venter et al., 2016b). PAs may be an effective tool to reduce the impacts of land-use disturbances, but recent evidence indicates that many PAs still experience considerable human impact (K. R. Jones et al., 2018). Moreover, protected and unprotected areas vary in their accessibility to people, which can be a strong measure of potential human impacts on wildlife from overexploitation and other disturbances (Deith & Brodie, 2020; Weiss et al., 2018). Before enhancing international commitments to PAs as a main conservation strategy, it is important to know whether existing PAs are counteracting pressures from increasing human footprint and accessibility, and thereby effectively helping achieve global biodiversity targets.

A key challenge to understanding contemporary drivers of biodiversity loss, and the effectiveness of conservation actions, is the relatively slow pace of biodiversity assess-

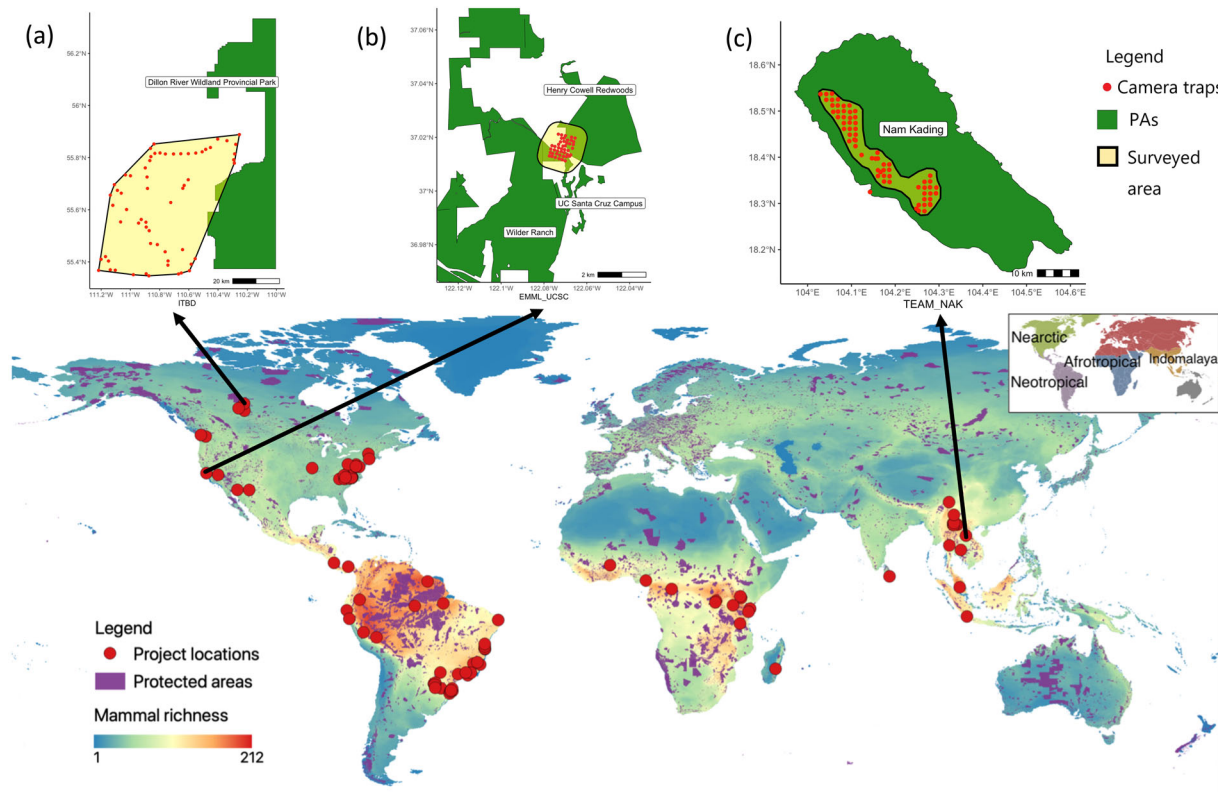
ments. For example, IUCN Red List assessments of a given species or group may be separated by 10 years or more (Mace et al., 2008). Clearly, more timely assessments of biodiversity status from standardized global observation systems are needed (Pereira et al., 2013). Recent advances in remote camera (camera trap) technology enable rapid monitoring of changes in the abundance and distribution of terrestrial vertebrate communities, especially for medium- and large-bodied terrestrial species. Despite the rapidly growing number of camera trap studies (Burton et al., 2015; Steenweg et al., 2017), relatively few have pooled data across a large number of sites to collaboratively address conservation questions at regional and global scales. Notable exceptions include regional evaluation of trends in occupancy (Beaudrot et al., 2016) and functional composition of mammal communities (Rovero et al., 2020), and similar large-scale assessments of carnivore assemblages and threatened species (Davis et al., 2018). These studies highlight the potential to further scale up camera trap data to inform global-scale analyses (Steenweg et al., 2017).

Here, we build on these efforts with a global evaluation of the relationships between mammal diversity and three key indicators of anthropogenic pressure: human footprint, human accessibility, and PA coverage (i.e., the proportion of an area under formal protected status). We assembled a dataset of mammal species occurrences and relative abundances from 91 camera trap surveys—covering areas inside and outside of PAs—across 23 countries on four continents (Figure 1) to evaluate the effectiveness of PAs at conserving mammal diversity, while controlling for other environmental factors. We evaluated two key dimensions of mammal diversity: taxonomic richness and functional diversity. While there has been much focus on the former, in terms of species extirpations and population declines (Ceballos et al., 2017), far less is known about how such declines affect the functional diversity of assemblages and the functioning of ecosystems (Gagic et al., 2015).

## 2 | MATERIALS AND METHODS

### 2.1 | Camera trap dataset and target species

We synthesized a global dataset of mammal detections from 91 camera trap surveys spanning four continents (Figure 1), including data from more than 8671 camera trap stations distributed inside and outside of PAs, collectively sampled for 752,039 camera trap-days (Table S1). These surveys include projects run by study authors and collaborators, previously published studies (Lima et al., 2017; Swanson et al., 2015), and surveys that were available



**FIGURE 1** Locations of 91 camera trap study areas from which mammal diversity was estimated, spanning 23 countries and four continents in different zoogeographic realms (inset; background richness from Jenkins et al., 2013). Three example camera trap surveys illustrate the gradient of camera trap sampling of protected area coverage (PA\_cov), from entirely outside (e.g., (a) Project ITBD, 1.42% PA\_cov), to partly within (e.g., (b) Project EMMML\_UCSC, 56.28% PA\_cov), to entirely within protected areas (e.g., (c) Project TEAM\_NAK, 100% PA\_cov)

through public databases (e.g., eMammal, Kays et al., 2020), implemented between January 2005 and August 2018. Surveys targeted medium- and large-bodied mammals (>500 g) with unbaited sampling and reported the number of total detections of each species. We used 400 camera days as a minimum per-survey sampling effort (Tobler et al., 2008). We also removed species that were unlikely to be consistently detected by cameras so as to reduce the potential influence of detection bias (see Supporting Information Methods for details).

## 2.2 | Biodiversity metrics

We calculated metrics of taxonomic diversity and functional diversity for each project. First, we calculated a relative abundance index (RAI) for each species in each study area as the number of independent detections per 1000 camera trap-days. Consecutive detections were considered independent if they contained different species or were of the same species but separated by more than a threshold time interval. Most of the studies used a threshold of 30–60 min for independence (O'Brien et al., 2003); where stud-

ies used a shorter threshold, we adjusted it to 30 min. We assumed that RAI reflected differences in relative abundances across species and surveys although we note that RAI may also be influenced by animal movement and detectability (Broadley et al., 2019), as are other metrics derived from camera trap detections (e.g., occupancy, Neilson et al., 2018). We calculated abundance-weighted diversity metrics as well as metrics based on presence–absence and examined the correlation between them.

For taxonomic diversity, we calculated the Shannon index (Magurran & McGill, 2011) using RAI for each species at each site, and also species richness (SR). For functional diversity, we calculated both Petchey and Gaston's dendrogram index for multiple traits (Petchey & Gaston, 2002), functional richness (Villéger & Moullot, 2008), and Petchey and Gaston's dendrogram index based on presence–absence data (FDPA) in the *fundiv* package (Gagic et al., 2015) in R statistical software (R Core Team, 2021), using four ecologically relevant traits for each species obtained from the PanTHERIA database (K. E. Jones et al., 2009) or other literature. The selected traits were adult body mass (g), trophic level (omnivore, herbivore, carnivore), activity cycle (diurnal, nocturnal,



both), and diet breadth (includes over 20 categories). For traits that were unavailable for a given species, we used values from the most closely related species (Brodie et al., 2021). We tested correlations among all biodiversity metrics; functional richness was correlated with taxonomic diversity (SR from presence–absence data, Pearson's  $r = 0.78$ ), and was therefore not considered in further analysis. Numerically, our biodiversity metrics were continuous variables bounded between  $-1$  and  $1$ .

### 2.3 | Environmental and anthropogenic variables

We collected spatial data for each project site to generate the predictor variables that we hypothesized would affect mammal diversity. To delineate the survey area for each project, we used one of three types of spatial information. First, we used the spatial extent (e.g., shapefile) of a project if it was provided by the data source. Otherwise, we created a minimal convex hull polygon around the set of camera points with a 500 m buffer (Figure 1). Multiple convex hull polygons were used when a study was conducted in different areas or there were distinct clusters of cameras. If we did not have shapefiles or camera locations, we used a circular polygon approximately covering the study area based on the longitude, latitude, and area reported by the project (for 14 of 91 projects; Supporting Information Methods).

We quantified three predictor variables to assess the relationships between mammal diversity and the degree of protection or pressure (Table 1; Figure S1a). For protection, we calculated the total percentage (%) of each study area polygon that overlapped with one or more PAs (of any IUCN category) in the World Database on Protected Areas (Table 1) (IUCN & UNEP-WCMC, 2014). We used this measure of PA coverage since projects spanned a range from having all cameras inside a PA, to some cameras inside and some outside, to all cameras outside (Figures 1 and 3; relatively fewer projects were partially inside and outside a PA; therefore, the variable had a bimodal distribution). To test the accuracy of this measure, we compared it with finer-scale measures for the subset of projects that reported camera locations, specifically with the percentage of PA overlap within 1 km and 500 m buffers around each camera trap. We found strong correlations between PA coverage based on the project-level convex hull polygons and the camera trap-level buffers (see Supporting Information Methods). Of all the PAs that overlapped with camera trap study areas, 11.5% were areas of stricter nature protection in IUCN categories Ia (1.7%), Ib (5.9%), and II (3.9%), while the other 88.5% were in categories III (22.0%), IV (3.4%), V (61.5%), and VI (1.6%), which allow more human activity (Day et al., 2012).

To estimate human impacts independently from PA coverage, we calculated the mean human footprint index within each survey area using the global human footprint map of 2009 (Venter et al., 2016a). The human footprint index provides a single metric accounting for the extent of built environments, croplands, pasture lands, human population density, electric infrastructure roads, railways, and waterways (Venter et al., 2016a). We also calculated the mean human accessibility score for each survey area using the global accessibility map (Weiss et al., 2018), which estimates travel time from a location to the nearest major city via surface transportation, including minor roads such as unpaved rural roads and exurban residential streets. Since the human accessibility index reflects travel time, a high value indicates low accessibility (i.e., higher remoteness).

We calculated additional covariates to control for environmental differences across camera trap survey areas (Table 1), specifically: annual average temperature (TEMP), average elevation (ELEV), zoogeographic realm (REALM), forest canopy height (CH), actual evapotranspiration (AET), and cumulative Dynamic Habitat Index (DHI) measured as the fraction of absorbed photosynthetically active radiation (fPAR), which is an indicator of vegetation productivity (details in Supporting Information Methods).

### 2.4 | Statistical analyses

We used linear and mixed-effects linear regression models to examine relationships between mammal diversity and human influence. Explanatory variables were assessed for collinearity using Pearson's correlation coefficient and were excluded if  $r > 0.6$  (AET was dropped due to high collinearity with other variables, see Supporting Information Methods; Table S2). We first built a core model with the environmental (nonanthropogenic) variables (Table 1) and compared it to other candidate models with these variables and all combinations of the human influence variables (Table S3). All continuous variables were standardized (mean = 0, variance = 1) to allow the direct comparison of effect sizes. We ran mixed-effects models with the global dataset where zoogeographic realm was treated as a random intercept for both abundance-weighted taxonomic diversity and functional diversity. To test whether there were different regional responses to human influence, we ran separate linear models (without a random effect) for data subsets from the four different zoogeographic realms: Nearctic, Neotropical, Afrotropical, and Indomalaya.

We used model selection to evaluate statistical support across candidate models based on Akaike's Information Criterion (AICc) adjusted for small sample sizes (Burn-

**TABLE 1** Predictor variables included in mixed effects linear models to explain global patterns of mammal taxonomic and functional diversity measured at camera trap survey sites. Spatial resolution, year of data collection, and data source are provided for each variable

Variable	Resolution (meter at equator)	Year of data collection	Data source
Human Influences			
Human footprint (HF)	1 km	2009	(Venter et al., 2016; <a href="https://doi.org/10.5061/dryad.052q5">https://doi.org/10.5061/dryad.052q5</a> )
Human accessibility (HA)	1 km	2015	(Weiss et al., 2018; <a href="https://www.map.ox.ac.uk/accessibility_to_cities">https://www.map.ox.ac.uk/accessibility_to_cities</a> )
Percentage of survey area within protected areas (PAcov)	Continuous variable	February 2019	World database on protected areas ( <a href="https://www.protectedplanet.net">https://www.protectedplanet.net</a> )
Environment			
Annual average temperature (TEMP)	1 km	2000	World-clim 2 ( <a href="http://www.worldclim.com/version2">http://www.worldclim.com/version2</a> )
Elevation (ELEV)	30 m	March 2019	ASTER GDEM ( <a href="https://asterweb.jpl.nasa.gov/gdem.asp">https://asterweb.jpl.nasa.gov/gdem.asp</a> )
Biogeographic			
Zoogeographic realm (REALM)	Shapefile	2013	(Holt et al., 2013; <a href="https://macroecology.ku.dk/resources/wallace">https://macroecology.ku.dk/resources/wallace</a> )
Habitat structure			
Fraction of absorbed photosynthetically active radiation based dynamic habitat indices (fPAR-based DHI)	1 km	2003–2014	MODIS ( <a href="http://silvis.forest.wisc.edu/data/dhis/">http://silvis.forest.wisc.edu/data/dhis/</a> )
Canopy height (CH)	1 km	March 2019	(Roll et al., 2015; Simard et al., 2011; <a href="https://webmap.ornl.gov/ogc/dataset.jsp?ds_id=10023">https://webmap.ornl.gov/ogc/dataset.jsp?ds_id=10023</a> )

ham & Anderson, 2002). Models with the lowest AICc, or within two AICc units of the best-fit model, were considered to have the most support. We used standardized regression coefficients and their 95% confidence intervals (CI) from the best (lowest AICc) model to assess the direction, magnitude, and statistical significance of estimated effect sizes. For variables not included in the best model, we used coefficients from the model with the next lowest AICc or from the FULL model if the variable in question was not included in any of the models of best-fit. To compare mixed-effects models with different fixed effects, we fitted, ranked, and weighted our models using maximum likelihood (ML) but then we estimated the variance component parameters using restricted maximum likelihood (REML; Luke, 2017; Zuur et al., 2009). We checked for normality and homogeneity of variance by visual inspection of residuals (Figure S3). We assessed goodness-of-fit by calculating marginal and conditional  $R^2$  for mixed-effects models using the *rsquared.GLMM* function (Barton, & Barton, 2015), or  $R^2$  for linear models using *summary* function. The

mean  $R^2$  across all best-fit models was 0.35 (range: 0.11–0.64; Table 2, Tables S4 and S5). All statistical analyses were performed using the *lme4* and *MuMIn* packages (Barton & Barton, 2015; Bates et al., 2015) in R statistical software version 4.1.1 (R Core Team, 2021).

### 3 | RESULTS

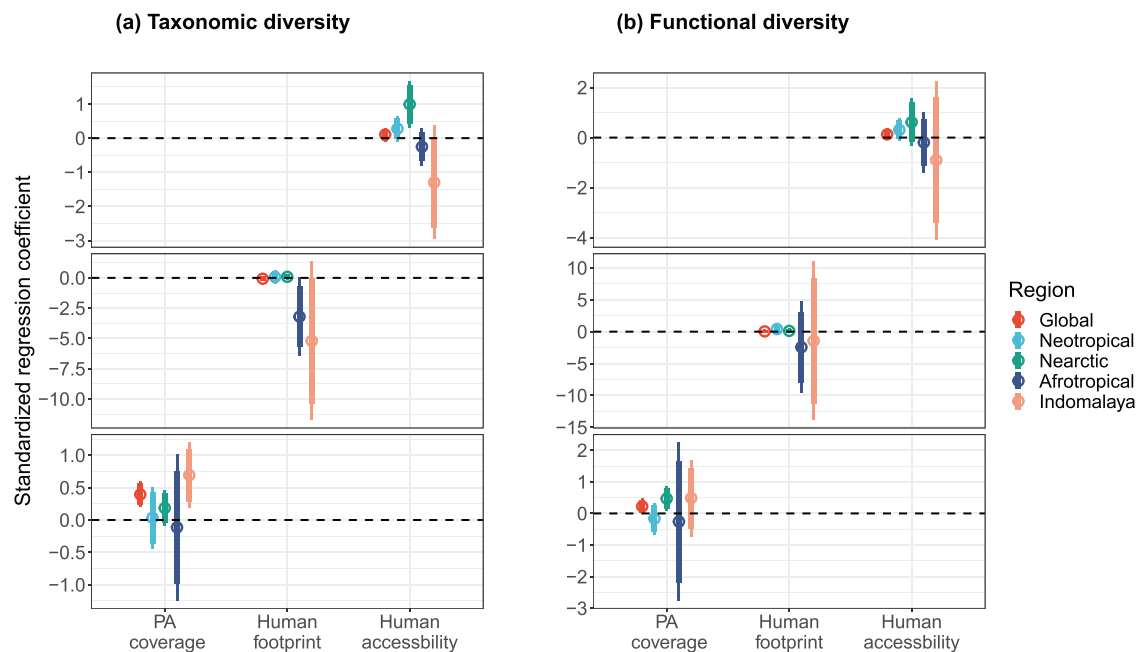
Globally, we found that mammal taxonomic diversity was positively associated with PA coverage (mixed-effects model:  $\beta = 0.39$ , 95% CI = 0.19–0.60), but not with human footprint or accessibility (Figures 2 and 3, Table S6). By contrast, mammal functional diversity was not significantly related to PA coverage at the global scale ( $\beta = 0.22$ , 95% CI = –0.02 to 0.46), nor to footprint or accessibility (Figure 2, Table S6). Taxonomic diversity was positively associated with elevation across the surveyed areas ( $\beta = 0.30$ , 95% CI = 0.13–0.48, Table S6), while functional diversity was negatively related to forest CH ( $\beta$

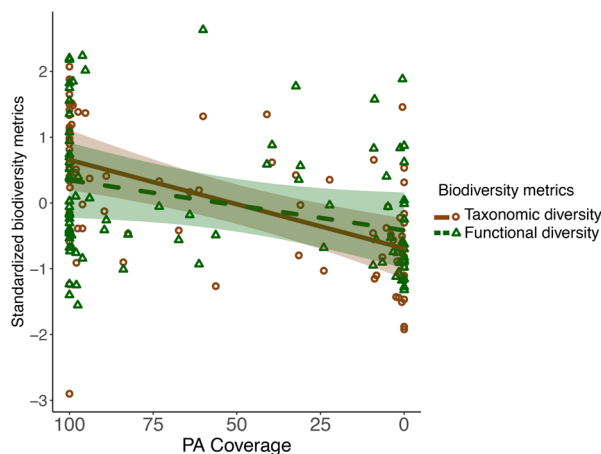
**TABLE 2** Model selection results and  $R^2$  for mixed effects linear models testing human influences on global taxonomic and functional diversity of mammals

Model names	AICc	$\Delta$ AICc	AICc weight	Marginal $R^2$	Conditional $R^2$
Taxonomic diversity (Shannon index)					
PAcov	<b>227.09</b>	<b>0</b>	<b>0.48</b>	<b>0.31</b>	<b>0.38</b>
HA_PAcov	<b>228.48</b>	<b>1.40</b>	<b>0.24</b>	<b>0.31</b>	<b>0.38</b>
HF_PAcov	<b>228.88</b>	<b>1.79</b>	<b>0.20</b>	<b>0.33</b>	<b>0.38</b>
FULL	230.77	3.69	0.08	0.32	0.38
HA	237.75	10.66	0	0.14	0.41
CORE	237.99	10.91	0	0.12	0.4
HF	238.78	11.70	0	0.14	0.37
HF_HA	239.61	12.52	0	0.14	0.39
Abundance weighted functional diversity (Petchey and Gaston)					
PAcov	<b>257.62</b>	<b>0</b>	<b>0.31</b>	<b>0.14</b>	<b>0.25</b>
HA_PAcov	<b>258.88</b>	<b>1.26</b>	<b>0.16</b>	<b>0.15</b>	<b>0.27</b>
CORE	<b>258.93</b>	<b>1.31</b>	<b>0.16</b>	<b>0.12</b>	<b>0.28</b>
HA	<b>259.33</b>	<b>1.71</b>	<b>0.13</b>	<b>0.13</b>	<b>0.3</b>
HF_PAcov	260.08	2.46	0.09	0.14	0.25
HF	261.06	3.44	0.06	0.12	0.26
FULL	261.37	3.75	0.05	0.15	0.28
HF_HA	261.82	4.2	0.04	0.13	0.3

Note: Bold values indicate which human influence variables best explained variation in mammal diversity (i.e., within two  $\Delta$ AICc of top-ranked models. Model names are specified in Table S3.

Abbreviations: HA, human accessibility; HF, human footprint; PAcov, protected area coverage.

**FIGURE 2** Regression coefficients ( $\beta$ ) for anthropogenic factors related to (a) taxonomic diversity (Shannon index) and (b) functional diversity, for mammal assemblages sampled from 91 camera trap study areas. For each estimate, circles denote the mean, thicker vertical lines show the 90% confidence interval, and thinner vertical lines extend to the 95% confidence interval. Estimates are from either the global model or submodels from the different zoogeographic realms



**FIGURE 3** Model-estimated relationships between the taxonomic diversity (Shannon diversity index, dark brown solid line) and functional diversity (dark green dash line) of mammals and protected area (PA) coverage. The colored line shows the mean prediction and the shaded area shows the 95% confident interval. Taxonomic diversity and functional diversity were predicted using parameters from the top global model for PA coverage (with other variables held at mean). Points represent project-specific values across the 91 camera trap surveys

$= -0.31$ , 95% CI  $= -0.53$  to  $-0.09$ ). The random effect of biogeographic realm explained little variance in the global model (0.06, compared to 0.6 residual variance). For both taxonomic and functional diversity, models with one or more indicators of human influence (PA coverage, human footprint, or human accessibility) had lower AICc and explained a similar or greater amount of variation ( $R^2$ , Table 2) as models including only environmental, habitat, and biogeographic covariates (CORE model, Table 2). Although, global SR and functional diversity based on presence-absence (FDPA) data were correlated ( $r = 0.90$ ), they responded differently to human influence. Species SR was significantly related to PA coverage ( $\beta = 0.26$ , 95% CI  $= 0.04$ – $0.48$ ) but not to human footprint or accessibility, while functional diversity was not significantly related to any human influences (Table S6). They were both positively associated with elevation (SR:  $\beta = 0.32$ , 95% CI  $= 0.13$ – $0.51$ , FDPA:  $\beta = 0.33$ , 95% CI  $= 0.12$ – $0.53$ ) and temperature (SR:  $\beta = 0.30$ , 95% CI  $= 0.06$ – $0.54$ , FDPA:  $\beta = 0.33$ , 95% CI  $= 0.06$ – $0.59$ ).

In the regional models, PA coverage was significantly related to mammal taxonomic diversity in Indomalaya ( $\beta = 0.69$ , 95% CI  $= 0.19$ – $1.2$ ) and functional diversity in Nearctic ( $\beta = 0.47$ , 95% CI  $= 0.09$ – $0.85$ ). Taxonomic diversity in the Nearctic was also positively related to the human accessibility index (i.e., to higher remoteness;  $\beta = 0.99$ , 95% CI  $= 0.31$ – $1.68$ ; Figure 2, Table S6). For the environmental factors, functional diversity in the Nearctic was negatively associated with temperature ( $\beta = -0.59$ , 95% CI  $= -0.94$  to

$0.25$ ), while taxonomic diversity in the Neotropical realm was positively associated with elevation ( $\beta = 0.52$ , 95% CI  $= 0.18$  to  $0.85$ ).

## 4 | DISCUSSION

The taxonomic diversity of terrestrial mammals is positively associated with coverage by PAs at a global scale, and this association is stronger than those between diversity and environmental factors or disturbances from human footprint and accessibility. This suggests that global efforts to create PAs have been worthwhile investments in biodiversity conservation, at least at current levels of human disturbances. While PAs are a cornerstone of conservation strategies, their effectiveness at conserving taxonomic and functional diversity has been questioned (Brum et al., 2017). In contrast to smaller-scale studies showing that variation in mammal communities was not associated with PA coverage (Brashares et al., 2001; Stewart et al., 2019), our results confirm the importance of PAs for global patterns of mammal diversity.

While we infer the positive association between mammal diversity and PAs to be indicative of conservation effectiveness, we note that the observed pattern could result if PAs were created in areas of higher biodiversity. However, previous studies have shown PAs to be disproportionately placed in economically marginal lands to reduce opportunity costs, rather than in the most biodiverse areas (Venter et al., 2018). A positive association between mammal diversity and PA coverage could be observed even if diversity is declining in PAs (Chen et al., 2019), necessitating an assessment of trends in diversity inside and outside of PAs, and ideally before and after their establishment, to more rigorously evaluate effectiveness. While previous work has demonstrated effective protection by PAs of forest cover (Naughton-Treves et al., 2005) and habitat structure (Geldmann et al., 2013; Joppa et al., 2008), our study indicates that those benefits extend to mammal communities. Long-term data to support such evaluation at a global scale are generally lacking, but previous studies do indicate that PAs facilitate vertebrate population persistence (Barnes et al., 2016) and prevent systematic declines in mammal diversity over the short term (Beaudrot et al., 2016). Future efforts must continue to build the evidence base from which the effectiveness of PAs for mammals and other components of biodiversity can be reliably monitored.

While our study represents the largest synthesis of camera trap surveys to date, there are many regional gaps in sampling coverage that may have influenced our results and remain to be filled by future research. For example, most of our surveys in the Afrotropical and Neotropical regions, where mammal diversity is naturally higher, were



in PAs, whereas half of the surveys in the less diverse Nearctic were outside PAs (Figure S1b). The Indomalayan surveys were relatively evenly distributed across a gradient of protected area coverage, but in this and the Afrotropical regions, sampling underrepresented areas of higher human footprint and accessibility (Figure S1b). More complete sampling coverage may thus improve on our results, and we echo previous calls and emerging efforts for more collaboration and coordination of camera trap research to help fill such gaps (Ahumada et al., 2020; Steenweg et al., 2017). More generally, we recommend coordinated sampling networks using biodiversity-sensing technologies, such as camera traps and acoustic recorders, that more evenly and comprehensively measure diversity across biomes and anthropogenic gradients, including direct experimental contrasts across conservation interventions like habitat protection.

We found mammal taxonomic diversity to be more strongly related to PA coverage than was functional diversity, suggesting that species-rich mammal communities associated with PAs also tend to have high functional redundancy (Cooke et al., 2019; Flynn et al., 2009; Mayfield et al., 2010). This may also be reflected in the negative association between functional diversity and CH, as high forest canopy promotes the packing of functionally similar species in biodiverse regions (Cooke et al., 2019; Feng et al., 2020). Such redundancy may mean that ecosystem functions provided by mammals could to some degree be resilient to species loss (Naeem, 1998), as has been documented for some other taxonomic groups (e.g., aquatic invertebrates; Schmera et al., 2012). However, the degree to which mammal assemblages can maintain their ecological functions in the face of increasing human impacts remains uncertain (Laliberté et al., 2010). Furthermore, an alternative explanation for the lack of an effect of PA coverage on functional diversity could be that while PAs have lost few species (i.e., maintain high taxonomic diversity), they may have lost functionally unique species that have also been lost outside PAs. For example, frugivores and herbivores can be disproportionately affected by hunting (Brodie et al., 2021), which still occurs in many PAs (Harrison, 2011) and would lead to declines in functional diversity that exceed those in taxonomic diversity. PAs in the Nearctic could be an exception: we found functional diversity in this region to be positively correlated with PA coverage, suggesting that North American PAs are effective at protecting functionally distinct species such as large mammals (Barnes et al., 2016; Loiseau et al., 2020).

It is notable that incorporating information on species abundances informed our inferences about mammal responses, as SR was not significantly correlated with PA coverage in our models based only on presence-absence

data. One explanation for this difference could be that species with high abundance contribute more to diversity, and thus the observed effects of PA coverage on mammal diversity could be driven by abundant species. Our analyses demonstrate the value of camera trap surveys in generating data on multispecies abundances within mammal communities, especially in the context of widespread declines in abundance (“biological annihilation”; Ceballos et al., 2017), although we acknowledge that further work is needed to develop and test robust estimators of abundance accounting for variation in detectability (Burgar et al., 2018; Gilbert et al., 2020).

Further work is also needed to better understand relationships between mammal diversity and human influences at regional scales, including the effects of human. Unlike some previous studies (e.g., Torres-Romero & Olalla-Tárraga, 2015), we only found a strong relationship between accessibility and diversity in the Nearctic region, which may be because the index we used (travel time from the nearest city) is a relatively coarse metric for many parts of the world. The scaling-up of more accurate and precise metrics of accessibility—such as from human movement models that incorporate population density, transportation networks, and landscape features (Deith & Brodie, 2020)—would facilitate more robust assessments of mammal responses to human access.

Overall, our results suggest that PAs are effective in conserving components of global terrestrial biodiversity. However, as human populations and consumption rates grow, so too do pressures in and around PAs. Encouragingly, about 60% of PAs in this study are categorized as IUCN type V, which permits more human use. This is consistent with previous findings that PAs focused on sustainable interactions between people and nature can retain more biodiversity than most unprotected areas (Gray et al., 2016), and is also aligned with our finding that diversity was not negatively related to human footprint and accessibility. It therefore remains critical to improve understanding of factors underlying current and predicted variation in the effectiveness of PAs and other area-based conservation measures (OECMs), such as community-managed forests (Nepstad et al., 2006) and Indigenous Peoples’ lands (O’Bryan et al., 2021). Research is particularly needed on the effectiveness of bottom-up and top-down governance structures, funding, management actions, and connectivity on PAs and OECMs (Maxwell et al., 2020; Packer et al., 2013).

With international attention moving beyond the Aichi targets to a post-2020 biodiversity framework (Visconti et al., 2019), there is an urgent need for reliable indicators of biodiversity change and rigorous assessments of conservation effectiveness. Our study highlights how camera trap surveys can generate standardized data on multispecies abundances within mammal communities across varied

ecosystems, thereby facilitating rapid assessments of global terrestrial vertebrate diversity (Kissling et al., 2018; Visconti et al., 2019), and ultimately supporting more effective conservation.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest interests.

## AUTHOR CONTRIBUTIONS

Cheng Chen and A. Cole Burton conceived the study and drafted and revised the manuscript. Cheng Chen and Runzhe Liu compiled and analyzed the data. Jedediah F. Brodie and T. Jonathan Davies contributed to conceptual development and drafting the manuscript. A. Cole Burton, Roland Kays, Jason T. Fisher, Jorge Ahumada, William McShea, and Douglas Sheil organized data collection and revised the manuscript. Bernard Agwanda, Mahandry H. Andrianarisoa, Robyn D. Appleton, Robert Bitariho, Santiago Espinosa, Melissa M. Grigione, Kristofer M. Helgen, Andy Hubbard, Cindy M. Hurtado, Patrick A. Jansen, Xuelong Jiang, Alex Jones, Elizabeth L. Kalies, Cisquet Kiebou-Opepa, Xueyou Li, Marcela Guimarães Moreira Lima, Erik Meyer, Anna B. Miller, Thomas Murphy, Renzo Piana, Rui-Chang Quan, Christopher T. Rota, Francesco Rovero, Fernanda Santos, Stephanie Schuttler, Aisha Uduman, Joanna Klees van Bommel, and Hilary Young, collected data and commented on the manuscript.

## DATA AVAILABILITY STATEMENT


Camera trap data obtained from eMammal (<https://emammal.si.edu>), TEAM (<https://www.conservation.org/projects/team-network>), now Wildlife Insights (<https://www.wildlifeinsights.org/>), and other sources listed in

Table 1. The replication data and code for mixed-effects linear regression model can be obtained from (<https://https://doi.org/10.5061/dryad.qfttdz0g2>).

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