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RESEARCH ARTICLE

Global disparity of camera trap research allocation and defaunation risk of terrestrial mammals

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Abstract

Quantifying and monitoring the risk of defaunation and extinction require assessing and monitoring biodiversity in impacted regions. Camera traps that photograph animals as they pass sensors have revolutionized wildlife assessment and monitoring globally. We conducted a global review of camera trap research on terrestrial mammals over the last two decades. We assessed if the spatial distribution of 3395 camera trap research locations from 2324 studies overlapped areas with high defaunation risk. We used a geospatial distribution modeling approach to predict the spatial allocation of camera trap research on terrestrial mammals and to identify its key correlates. We show that camera trap research over the past two decades has not targeted areas where defaunation risk is highest and that 76.8% of the global research allocation can be attributed to country income, biome, terrestrial mammal richness, and accessibility. The lowest probabilities of camera trap research allocation occurred in low-income countries. The Amazon and Congo Forest basins – two highly biodiverse ecosystems facing unprecedented anthropogenic alteration – received inadequate camera trap research attention. Even within the best covered regions, most of the research (64.2%) was located outside the top 20% areas where defaunation risk was greatest. To monitor terrestrial mammal populations and assess the risk of extinction, more research should be extended to regions with high defaunation risk but have received low camera trap research allocation.

Introduction

We are experiencing a biodiversity crisis with estimated global extinction rates 100–1000 times greater than pre-human rates (Chapin et al., 2000; Christie et al., 2020; IPBES, 2019). Mammals have experienced some of the highest species (Ceballos et al., 2015; IPBES, 2019; Purvis et al., 2019). These extinctions have often been preceded and catalyzed by dramatic declines in mammal abundance and population extirpations (Benitez-Lopez et al., 2017; Ceballos et al., 2017; Dirzo et al., 2014; Ripple et al., 2015; Williams et al., 2022). The decline and loss in mammal species abundance have been termed "defaunation" – the human-driven depletion of wild animals (Giacomini & Galetti, 2013). Defaunation is highest for terrestrial mammals (Allan et al., 2019; Ceballos et al., 2020; McCauley et al., 2015). The broader impacts of defaunation include cascading effects on other species (Estes et al., 2011; Ripple et al., 2014, 2015), forest carbon storage (Bello et al., 2015), and natural forest regeneration (Gardner et al., 2019).

The risk of ecosystems to defaunation is well documented (Geldmann et al., 2019; Harfoot et al., 2021; Jones et al., 2018; Williams et al., 2022; Wolf et al., 2021). Global priorities to identify and mitigate the risk of defaunation have been developed (Cazalis et al., 2022; Harfoot et al., 2021; Leadley et al., 2022; Williams et al., 2022). Global biodiversity indicators and monitoring tools such as the International Union for Conservation of Nature (IUCN) Red List of Threatened Species

(Cazalis et al., 2022), the Red List Index (Butchart et al., 2006), the Living Planet Index (Collen et al., 2009), and the Wildlife Picture Index (Beaudrot et al., 2016; O'Brien et al., 2010) have also been introduced.

However, the international community has struggled to effectively assess and monitor population trends and thus track progress toward mitigating defaunation, primarily because biodiversity indicators and monitoring tools require *in situ* primary data on terrestrial mammals to be able to track population trends (Cazalis et al., 2022; Collen et al., 2009; O'Brien et al., 2010). Even for the most assessed taxa on the IUCN Red List of Threatened Species, mammals, 16% of the assessed species, are classified as Data Deficient (Cazalis et al., 2022; IPBES, 2019). The conservation community, therefore, acknowledges that the assessment and monitoring (research) of mammals are crucial to track defaunation and evaluating conservation effectiveness (Anderson, 2018; Beaudrot et al., 2016; Bush et al., 2017; Cazalis et al., 2022; IPBES, 2019; Kuhl et al., 2020). But research on terrestrial mammals is difficult because they often occur at low densities and can be challenging to detect (Ahumada et al., 2011; Bush et al., 2017).

For over two decades, camera traps have revolutionized the way scientists and conservation stakeholders survey terrestrial mammals, as camera traps operate continuously for months at a time without the need for observer presence (Ahumada et al., 2011; Beaudrot et al., 2016; Rovero & Ahumada, 2017; Semper-Pascual et al., 2022; Tilker et al., 2019). However, we do not understand how anthropogenic activities often posing direct threats to terrestrial mammals, biodiversity, economics, and geography determine relative camera trap research allocation and if camera trap research is conducted in areas that face the greatest defaunation risk. Previous attempts to understand biodiversity research allocation and its correlates compared either the number of published studies (Hickisch et al., 2019; Lawler et al., 2006; Wilson et al., 2016) or research impact (Meijaard et al., 2015) among biomes (Christie et al., 2020) or countries and their constituent provinces. However, the quantity of research in these previous studies was tied to a country (and provinces) or biome. It did not reveal the nuances in research allocation across countries, biomes, or the global landscape.

Here, we assessed the global allocation of camera trap research on terrestrial mammals (hereafter "camera trap research") using an established geospatial distribution modeling approach (maximum entropy, "MaxEnt") (Elith et al., 2011; Phillips et al., 2006). We combined a dataset of camera trap research locations on terrestrial mammals published between 2000 and 2019 (see "Materials and Methods" section; Fig. 1) with 10 spatial datasets (hereafter "predictors") representing anthropogenic, biological, economic, and topographic factors thought to relate to camera trap research allocation (Table S1). We limited our scope to camera trap research on terrestrial mammals because they are disproportionately impacted by anthropogenic activities and face a high defaunation risk (Allan et al., 2019; Ceballos et al., 2020; McCauley et al., 2015; Schipper et al., 2008; Williams et al., 2022). Our goals were to (1) document terrestrial mammal camera trap research allocation and characterize its global distribution, (2) identify predictors of global camera trap research allocation, and (3) assess camera trap research allocation in relation to terrestrial mammal defaunation risk.

Materials and Methods

A systematic search of camera trap studies

On 09.09.2019, we conducted an extensive systematic literature search on the Web of Science™ (Science Citation Index Expanded) and Google Scholar databases for both peer-reviewed and gray literature published between 1900 and August 2019 that used camera traps as a research tool. We followed standard guidelines for conducting a systematic literature search in conservation and environmental management (Pullin & Stewart, 2006). We used *a priori* selected search string: (camera trap* OR camera-trap* OR remote camera* OR photo trap* OR photo-trap* OR camera NEAR/1 trap* OR trail camera* OR automatic camera* OR remotely triggered camera* OR game camera* OR motion-activated camera* OR infrared camera* OR wildlife camera*) AND (wildlife* OR animal* OR mammal* OR vertebrate* OR terrestrial vertebrate*). For the Web of Science, we specified the search within the biological research categories: environmental sciences, ecology, zoology, biodiversity conservation, behavioral sciences, forestry, evolutionary biology, remote sensing, reproductive biology, and anthropology.

We checked the searches returned from Web of Science and Google Scholar for duplicate records and those not in English, which we removed (Burton et al., 2015; Lawler et al., 2006). In the WoS, we searched "All fields" in the following databases: Web of Science Core Collections, Book Citation Index, Current Contents Connect, Data Citation Index, Derwent Innovation Index, Korean Journal Database, MEDLINE, Russian Science Citation Index, SCIELO, Zoological Record, Data Citation Index, SciELO Citation Index, and BIOSIS Citation Index. We then downloaded the studies as .pdf, MS Word, or HTML files. Using the title, abstract, and main text, we identified studies based either wholly or in part on-field use of camera traps to study terrestrial mammals for ecological and/ or conservation research purposes. We then subjected these studies to *a priori*-designed inclusion/exclusion

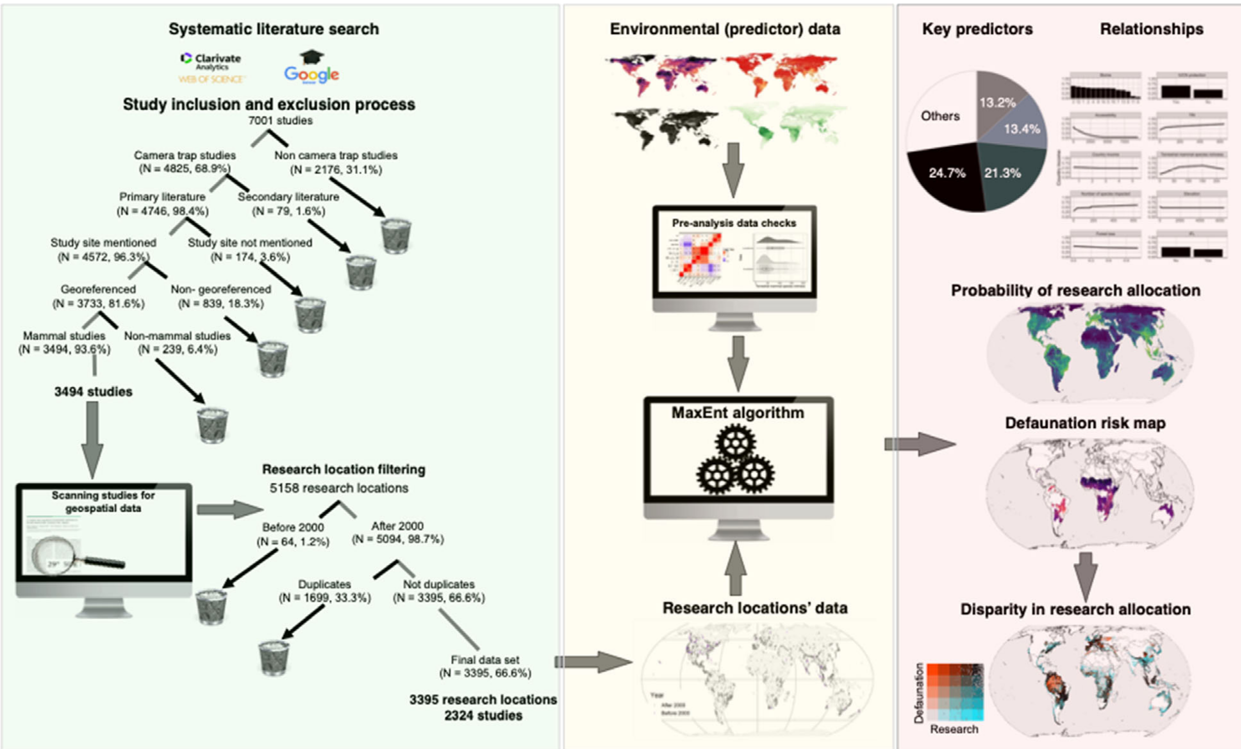

Figure 1. Step-by-step schematic representation of data collection and modeling workflow.

criteria (Fig. 1). We used the duplication function in Ms. Excel to identify and exclude duplicate records. We then excluded books, book chapters, and reviews because (1) they rarely report primary *in situ* camera trap data and (2) we could not access copies which was necessary to extract study-specific location information. We also excluded studies that did not provide camera trap research location name(s), those that provided research location name(s) but either the location could not be georeferenced, or the geospatial information (longitude and latitude) was erroneous, and finally studies on non-mammalian terrestrial wildlife. In the remaining studies, we extracted the location information (longitude and latitude) where the study was conducted. We excluded research locations for studies conducted before the year 2000 to ensure that research location data matched the temporal extent of the predictors. We also removed duplicated locations.

Collating and processing of predictor datasets

Based on our research experience, study objectives, and published literature, we selected 10 environmental predictors for their potential importance to camera trap research location selection and terrestrial mammal defaunation (Table S1). The predictors included: country income, IUCN protected area, forest loss, number of species impacted by human activity, terrestrial mammal diversity, remoteness, Intact Forest Landscape, biome, elevation, and Terrain Ruggedness Index. A detailed description of the covariate datasets is given in Table S1.

We processed the geospatial data in the R statistical language (R Core Team, 2019). Because our predictors' data originated from different sources, we harmonized projections, grid cell size and alignment, and the spatial extent to ensure consistency across all predictor data layers using appropriate functions from the "raster" package (Hijmans, 2020). We chose a geographical latitude/longitude projection at 30 arc-second resolution (*c.* 1 km at the equator) for this analysis. We plotted the research location data on a global map to locate where camera trap research has been conducted. We used the *extract* function of the "raster" package to extract the raster values to allow us to compute a Spearman's rank correlation matrix to test for multi-collinearity among predictors (Figure S1). We assumed predictors with a correlation value $r < -0.7$ or $r > 0.7$ to be correlated. None of our six continuous predictors were collinear, and all were included in the subsequent models. We then used the *spsample* function and the Fibonacci sampling type argument in the "sp" package (Pebesma & Bivand, 2005) to create 50 000 random points for which, together with each camera research location, we extracted the associated predictor data. This allowed us to compare the predictor data distribution at camera trap research locations with random locations across the landscape. We used the "ggplot2" R package (Wickham, 2016) to visualize the data distribution of the continuous and categorical predictors, respectively, between camera research locations and a random sample of the available land surface (Figure S2).

MaxEnt modeling

We used the MaxEnt models to (1) identify the key predictors of camera trap research allocation and (2) predict the spatial probability for camera trap research allocation, given the relationship between research allocation and predictors. We implemented the MaxEnt models using the *maxent* function in the "dismo" package in R (Hijmans et al., 2017). Before modeling, we used the *ENMevaluate* function in the "ENMeval" package to tune our models, i.e., identify the optimal feature classes and regularization multiplier values needed to maximize model predictive ability while avoiding overfitting (Muscarella et al., 2014). We split the camera trap research locations into two separate partitions (80% for model training and 20% for model testing). We ran five MaxEnt models. (1) One global model (using all camera trap research locations) and (2) four biome-specific models for biomes with the highest number of camera trap research locations (hereafter, "most camera trap researched biomes"). We used feature classes and the regularization multiplier value of the model with the lowest Akaike information criterion value as returned by the *ENMevaluate* process. We set the number of background points to 10 000 for all models. We used the value of the area under the curve (AUC) of the receiver operating characteristic curves on the test data to assess model performance. We assumed models with an AUC value of >0.70 to be of good model fit (Phillips et al., 2006). We used the jackknife procedure and permutation importance to assess variable importance and to identify the most important predictors of camera trap research allocation (Phillips et al., 2006).

Quantifying disparity *in camera* trap research location selection and defaunation risk

We used bivariate choropleths to assess the relationship between the probability of camera trap research allocation and defaunation risk at the four most camera trap researched biomes. We first developed a "defaunation risk map" for each biome to identify areas of defaunation risk (ranging between 0 and 1) across the landscape. We generated the defaunation risk map by following these steps. (1) We identified from our set of predictors those related to defaunation risk: number of terrestrial mammals impacted by human activities (Allan et al., 2019), forest loss (Hansen et al., 2013), and terrestrial mammal richness (Jenkins et al., 2013). (2) We normalized the predictors (from step 1) to range from 0 to 1. (3) We combined the normalized predictors (from step 2) into one map as a raster stack using the *stack* function in the "raster" package (Hijmans, 2020). (4) We created equal weights to apply to all predictors (the raster stack from step 3). We used equal weights to avoid any subjective representation of one or more covariates in the derived defaunation risk map. (5) We then used the *weighted.mean* function in the "raster" package (Hijmans, 2020) to calculate the defaunation risk map as a weighted mean (using the weights from step 4) for the combined predictors. (6) Lastly, we used the *writeRaster* function in the "raster" package to export the defaunation risk map.

To generate a bivariate choropleth, we used a customized R function that divided the probabilities of camera trap research allocation and the defaunation risk datasets into five classes, each containing 20% of the available values (quintiles). The bivariate choropleth indicates the spatially explicit strength of associations between two variables and results in (1) high–high values, here, areas with high defaunation risk and high predicted probability of camera trap research allocation, (2) high–low values, high defaunation risk, and low predicted probability of research allocation, (3) low–high values, low defaunation risk and high predicted probability of research allocation, and (4) low–low values, low defaunation risk, and low predicted probability research allocation. We then used the *extract* function of the "raster" package to extract the defaunation risk quintile for each of the research locations in the four most camera trap researched biomes. We used the accruing data to calculate the percentage of camera trap research locations in each defaunation risk quintile.

Results

Searches from Web of Science and Google Scholar returned 4350 and 7047 studies, respectively. After removing duplicate studies and those not in English, we obtained a combined list of 7001 studies. From the 7001 studies, we excluded 2176 as non-camera trap studies, and 79 books, book chapters, and reviews. In the remaining 4746 records, we excluded 174 studies that did not provide research location name(s), 839 studies that provided research location name(s), but either the location could not be georeferenced or the geospatial information (longitude and latitude) was erroneous, and 239 studies on non-mammalian terrestrial wildlife. We thus retained 3494 studies for which we extracted the studies' longitude and latitude information. As some studies involved multiple locations, 5158 research locations were identified. We then excluded 64 research locations for studies conducted before 2000 to ensure that research location data matched the temporal extent of the predictors. We also removed 1699 duplicated locations. We thus remained with 3395 camera trap research locations from 2324 studies for use in the subsequent analyses.

The most camera trap researched biomes were Tropical and Subtropical Moist Broadleaf Forests (hereafter "tropical moist forests", $n = 1075$); Temperate Broadleaf and Mixed Forests (hereafter "temperate forests", $n = 711$); Tropical and Subtropical Grasslands, Savannas, and Shrublands (hereafter "tropical grasslands", $n = 311$); and Mediterranean Forests, Woodlands, and Scrub (hereafter "Mediterranean biome", $n = 228$). The discriminative performance of our models gave an average model AUC measure of ≥ 0.8; hence, the models were useful in identifying the most important predictors (Table S2) and specific areas of camera trap research allocation (Figs. 3 and 4).

Global patterns of camera trap research allocation

We observed an increase in the number of published camera trap studies on terrestrial mammals (Fig. 2A) and the number of countries hosting such studies (Fig. 2B). Camera trap research was conducted in 130 countries (Fig. 2C). The countries with the most research locations (in descending order) were the USA, Brazil, Australia, India, Mexico, China, and Malaysia (Fig. 2D; Table S2). Among large countries (area >1 million km^2), Mauritania, the Democratic Republic of Congo, Niger, Angola, Libya, Kazakhstan, Algeria, Ethiopia, and Egypt received fewer than five research studies each (Table S2). Singapore, Belize, Mauritius, Costa Rica, and Panama hosted the highest density of studies (Fig. 3C; Table S2). North America, continental Europe, the United Kingdom, and Japan had a high probability of research allocation

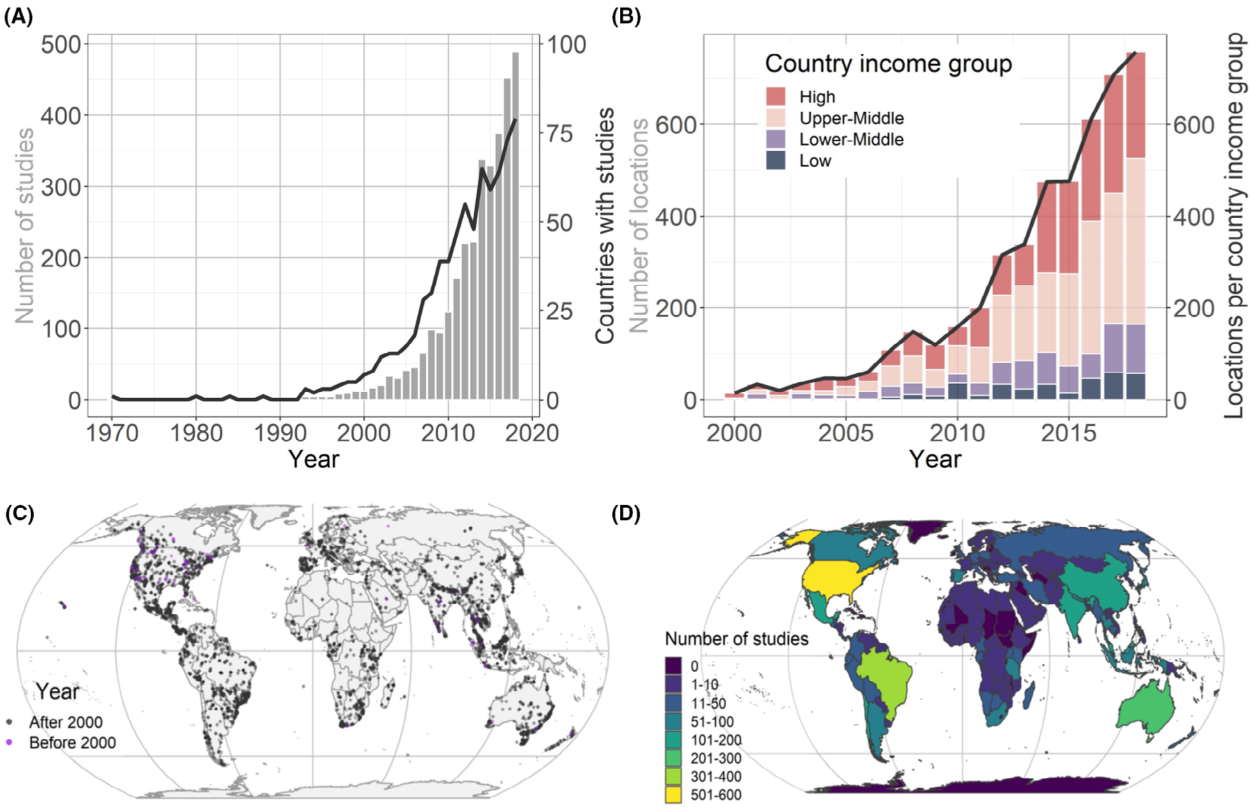

Figure 2. Temporal and spatial patterns of camera trap research. (A) Number of studies that used camera traps as a research tool (left axis and bar graph) and number of countries where the research was conducted (right axis and line graph) between 1970 and 2019. (B) Number of locations in the past two decades (right axis and line graph) compared among country income groups (left axis and stacked bar graph). (C) Global research locations before and after year 2000. (D) Number of studies that used camera traps as a research tool per country.

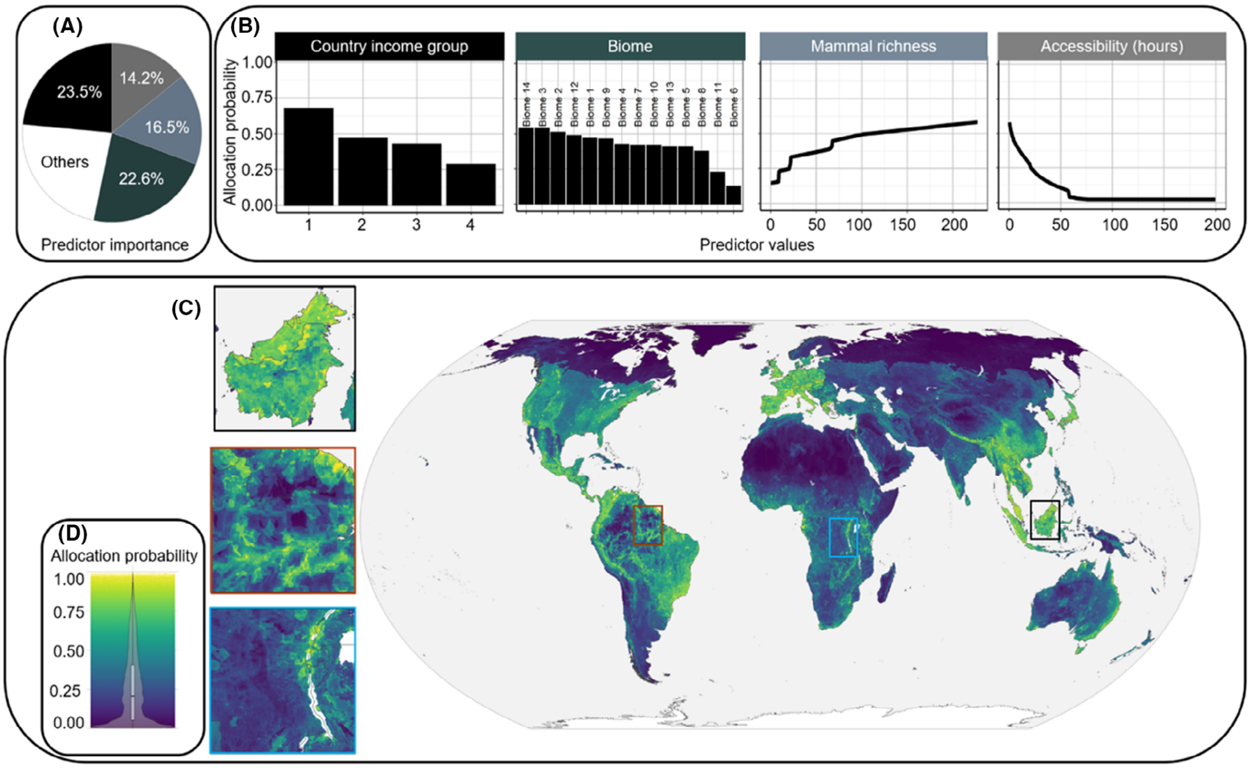

Figure 3. The most important predictors of global research allocation. (A) Permutation importance of the top four predictors (and others combined). (B) Relationships between the probability of research allocation and the top four most important predictors. (C) Probability of research allocation and three zoomed-in areas (insets) of the tropical moist forest biome: Southeast Asia (Borneo), South America (Amazon), and Africa (Congo Basin). (D) Violin plot showing the probability of research allocation values and the color ramp as a legend for the maps. The violin plot shows the median and the interquartile range of the probability of research allocation. The biomes are as follows: *1 = Tropical and Subtropical Moist Broadleaf Forests*, *2 = Tropical and Subtropical Dry Broadleaf Forests*, *3 = Tropical and Subtropical Coniferous Forests*, 4 = Temperate Broadleaf and Mixed Forests, 5 = Temperate Conifer Forests, 6 = Boreal Forests/Taiga, 7 = Tropical and Subtropical Grasslands, Savannas and Shrublands, 8 = Temperate Grasslands, Savannas and Shrublands, 9 = Flooded Grasslands and Savannas, 10 = Montane Grasslands and Shrublands, 11 = Tundra, *12 = Mediterranean Forests, Woodlands, and Scrub*, 13 = Deserts and Xeric Shrublands, and *14 = Mangroves*. The top five biomes with the highest probability of research allocation in italics.

(Fig. 3C). In comparison, African countries generally had some of the lowest probabilities (Fig. 3C; Table S2).

The biomes with the highest density of camera trap research, research locations, and predicted probability of research allocation were mangroves, Tropical and Subtropical Coniferous Forests (hereafter "tropical coniferous forests"), Mediterranean biome, tropical moist forests, Tropical and Subtropical Dry Broadleaf Forests (hereafter "tropical dry forests") (Fig. 3B; Table S3). Boreal forests/Taiga and Tundra biomes had the lowest density of camera trap studies and predicted probability of research allocation (Fig. 3B; Table S3).

Within the tropical moist forests biome, we predicted a higher probability of camera trap research allocation in Malaysia, Thailand, and Indonesia. In comparison, tropical African countries had a much lower probability of research allocation (Fig. 4C). In South and Central America, the Brazilian Atlantic dry forests had the highest probability of research allocation (Fig. 4C). In the tropical grassland biome, the Cerrado and the Llanos in Colombia and Venezuela had the highest probability of research allocation (Fig. 4C). Apart from South Africa and some areas in East Africa, African savannahs, grasslands, and shrublands had a disproportionally low probability of research allocation. In contrast, grasslands and shrublands in Australia had a higher probability of camera trap research allocation (Fig. 4G). In the Mediterranean biome, California, South Africa, and Southern Europe, particularly Italy, Greece, and southern France, had a higher probability of research allocation (Fig. 4). Lastly, in the temperate forests biome, Japan, the United Kingdom, and South-Eastern Australia had the highest probability of research allocation. In contrast, areas in Eastern Europe and those in Russia or the Caspian region had a lower probability of research allocation (Fig. 4O).

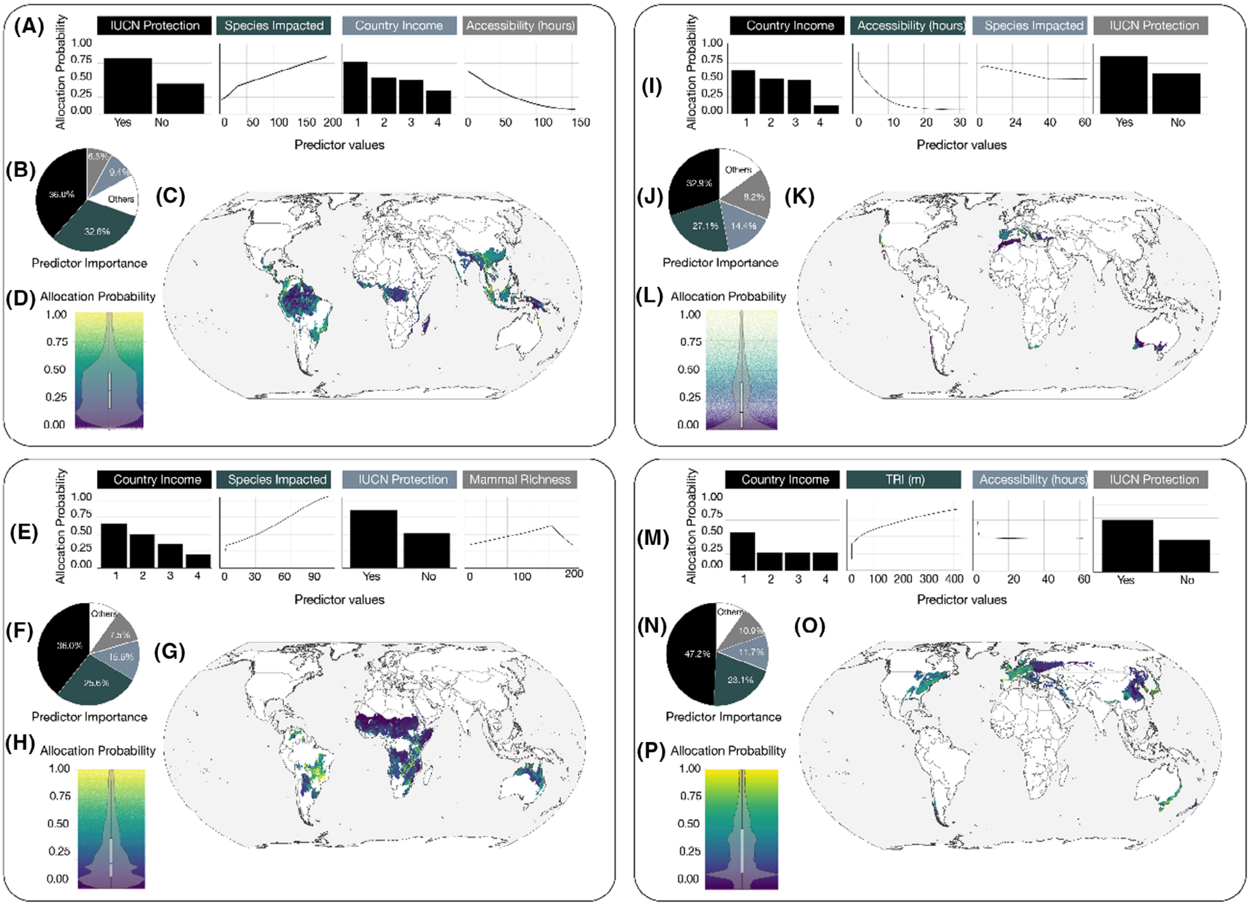

Figure 4. The most important predictors and probability of research allocation in the four most researched biomes: the tropical moist forests (top left), tropical grasslands (bottom left), Mediterranean forests (top right), and temperate forests (bottom right). (A, E, I, M) Relationships between the probabilities of research allocation and the top four most important predictors. (B, F, J, N) Permutation importance of the top four predictors (and others combined). (C, G, K, O) Probability of research allocation for each of the biomes. (D, H, L, P) Violin plots showing the probabilities of research allocation values for each of the four biomes also used here as a legend. The violin plots show the median and the interquartile range of the probability of research allocation.

Predictors of camera trap research allocation

Globally, country income was the most important predictor of camera trap research allocation, describing 23.5% of the variability in predicted camera trap research allocation, followed by biome (22.6%), terrestrial mammal richness (16.5%), and accessibility (14.2%) (Fig. 3A). Country income decreased the global model AUC the most when omitted, suggesting that it has the most important information that is not present in the other predictors (Figure S4A). The probability of camera trap research allocation was higher in high-income countries and lower in low-income countries (Fig. 3B). Among biomes, the probability of camera trap research allocation was higher in the mangroves, tropical dry forests, tropical coniferous forests, Mediterranean biome, and tropical moist forests. Boreal forests/Taiga and Tundra biomes had the lowest probability of camera trap research allocation (Fig. 3B). There was a strong positive trend in camera trap research allocation with terrestrial mammal richness and accessibility (Fig. 3B).

In addition to the global analysis, we analyzed the four most camera trap-researched biomes independently to get further insights into the biome-specific predictors. Country income and IUCN-protected area status were the only predictors consistent in all four biomes (Fig. 4A, E, I, and M; Table S4), with camera trap research allocation being twice as high within protected areas than outside. Accessibility was a key predictor in three (tropical moist forests, Mediterranean biome, and temperate forests) of the four most researched biomes, with higher camera trap research allocation in more accessible areas (Fig. 4A, I, and M; Table S4). The number of terrestrial mammals impacted by human activity was a key predictor in three (tropical moist forests, tropical grasslands, and Mediterranean biome) of the four most researched biomes (Fig. 4A, E, and I; Table S4). There was a positive trend toward more camera trap research allocation in areas with a higher number of terrestrial mammals impacted by human activity, particularly in the two tropical biomes (Fig. 4A and E). In contrast, the trend was less clear in the Mediterranean biome (Fig. 4I). Lastly, terrestrial mammal richness, which had a clear positive trend at the global level (with high species richness areas receiving a higher camera trap research allocation, Fig. 3B), was a key predictor only in the tropical grasslands (Fig. 4E). In line with the global trend, we saw a general trend toward more camera trap research in more terrestrial mammal species-rich landscapes. However, compared to the global level, research allocation in the grassland regions decreased again above 160 mammal species (Fig. 4E).

Disparity in research allocation and terrestrial mammal defaunation

Of the total number of camera trap research locations in the tropical moist forests biome, 42.8% (n = 448) of those were in the top 20% areas with the highest defaunation risk (Fig. 5C and E); 54.3% (n = 168) in the tropical grasslands biome (Fig. 5C and G); 20.8% (n = 47) in the Mediterranean biome (Fig. 5C and I); and 25.1% (n = 174) in the temperate forests biome (Fig. 5C and K). On the other hand, 5.1% (n = 54) of all locations in

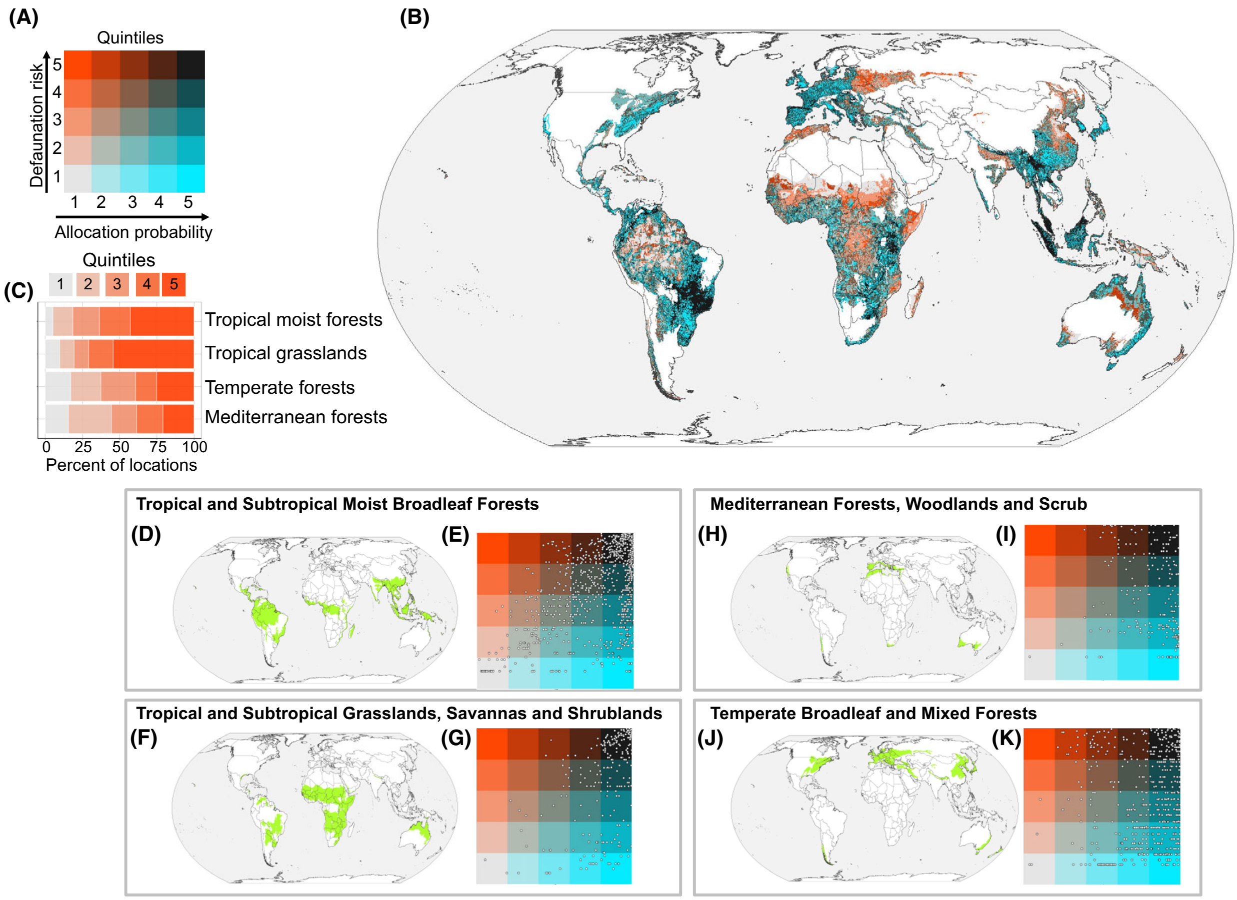

Figure 5. Disparity in the probability of camera trap research allocation and the terrestrial mammal defaunation risk. (A) Bivariate choropleth showing the relationship between the probability of research allocation and the defaunation risk. Numbers 1–5 on the bivariate choropleth depict quintiles. Each color change means a 20% quintile change in the probability of camera trap research allocation and defaunation risk. (B) Disparity in the probability of camera trap research allocation and defaunation risk. Notable, areas in orange are of high defaunation risk. These areas would be the best targets for camera trap research aimed at informing strategies to mitigate defaunation risk. (C) Percentage of camera trap research locations in quintiles of high defaunation risk areas. (D, H, F, J) Depict the extent of the four most camera trap researched biomes; tropical moist forests, tropical grasslands, Mediterranean forests, and temperate forests. (E, I, G, K) Depict legends for the bivariate choropleth in (A); overlaid with research locations (dots).

the tropical moist forests biome were in the 20% areas with the lowest defaunation risk (Fig. 5C and E); 9.7% (n = 30) in the tropical grasslands biome (Fig. 5C and G); 15.5% (n = 35) in the Mediterranean biome (Fig. 5C and I); and 17.2% (n = 119) in the temperate forests biome (Fig. 5C and K). Overall, 64.2% of the research in the four most researched biomes was located outside the top 20% areas where defaunation risk was greatest.

We observed high camera trap research allocation in areas of the Brazilian Atlantic dry forests and large parts of Southeast Asia (particularly Indonesia, Singapore, and Malaysia) facing the highest defaunation risk (Fig. 5B). But there was a disparity in research allocation and defaunation risk, particularly in Eastern Europe, Russia, the Caspian region, and some areas of Africa, including Liberia, the Central African Republic, and the Democratic Republic of the Congo, all regions have a high defaunation risk (Figure S5) but received low camera trap research allocation (Fig. 5B).

Discussion

Our results indicate that camera trap research increased over time (Fig. 2A), albeit with distinct spatial biases (Figs. 3–5). These biases are apparent at the global and biome levels and appear primarily associated with country income. Only a minor amount was associated with predictors such as forest loss, terrestrial mammal species richness, and number of terrestrial mammals impacted by human activity. On the one hand, the increase in and widespread allocation of camera trap research underlines the increasing role of camera trap research, and on the other hand, the allocation indicates limited attention to the processes of defaunation and the locations where the risks are most severe.

At the country level, the probability of research allocation was highest in high-income countries and lowest in low-income countries. The importance of country income for research allocation is in contrast to the assumption that research location selection should target areas of greatest defaunation risk. Many of the world's most biodiverse and high-defaunation risk regions occur in the lower middle- and low-income countries where much of the current global environmental degradation and associated defaunation is concentrated (Allan et al., 2019; Benitez-Lopez et al., 2019; Ceballos et al., 2020; Curtis et al., 2018; Hansen et al., 2020; IPBES, 2019; Tilker et al., 2019). A notable example is the Congo Basin forests, which are impacted by road expansion, mining, intensive timber extraction, commercial hunting and other developments (Batumike et al., 2021; Giljum et al., 2022; Kleinschroth et al., 2019), along with unprecedented smallholder clearing for agriculture associated with increasing human population (Tyukavina et al., 2018). Such developments offer financial gains in a region suffering severe poverty, but without care this has negative implications for biodiversity conservation and attaining the conservation targets (Edwards et al., 2014; Kleinschroth et al., 2019).

The importance of country income for conservation is well established (Barbier et al., 2018; Lindsey et al., 2018; Meijaard et al., 2015; Moussy et al., 2022; Wolf et al., 2021). For example, ineffective protected area management is often associated with insufficient equipment, staff, and other financial resources within poorer nations (Appleton et al., 2022; Coad et al., 2019; Lindsey et al., 2018; Wolf et al., 2021). Our observation that research allocation differs among country income groups corroborates the important role of financing in global biodiversity conservation (Meijaard et al., 2015; Moussy et al., 2022; Waldron et al., 2013). High-income countries typically invest more in scientific research, foster innovation and technological advancement, and have established scientific infrastructure, expertise, training, and a long-term tradition and culture of scientific inquiry (Meijaard et al., 2015; Waldron et al., 2013).

Country income is associated with other factors that may influence research activities, including political stability, good governance, safety and security, the presence of strong domestic research programs and institutions, and infrastructure development (e.g., availability of research stations among others). Accessibility, for example, is limited in many low-income countries (Weiss et al., 2018), making areas critical for conservation in these countries hard to reach for researchers. This is clearly seen in our findings insofar as research allocation probability decreased rapidly with accessibility both at the global level (Fig. 3) and in three of the four most researched biomes (Fig. 4A, I, and M). From a conservation perspective, effort and allocation should reflect conservation needs and biological interests rather than the country's wealth (Meijaard et al., 2015).

Biome-specific biases in conservation allocation have previously been reported in identifying global conservation priority areas (Lovejoy, 2020; Strassburg et al., 2020), allocating conservation research (Meijaard et al., 2015; Wilson et al., 2016), research funding allocation (Lovejoy, 2020) and in the establishment of protected areas (Hoekstra et al., 2005; Jenkins & Joppa, 2009). This likely reflects how both biological diversity and the level of threats differ among biomes (Dinerstein et al., 2017; Lawler et al., 2006). Currently, we see a shift in conservation priorities from threatened species to threatened biomes (Hoekstra et al., 2005). For example, the IUCN-protected area coverage, as a cornerstone for biodiversity conservation (Tilman et al., 2017; Wolf et al., 2021), has expanded in the last decades as part of the overall global increase in conservation allocation in the biomes at risk (Hoekstra et al., 2005; Jenkins & Joppa, 2009; Wolf et al., 2021). We also recorded high camera trap research location densities and probabilities of research allocation in some of the biomes at risk (Hoekstra et al., 2005; Jenkins & Joppa, 2009); Mediterranean biome; tropical dry forests; tropical coniferous forests; and tropical moist forests. This finding brings optimism that regions facing the highest anthropogenic threats are receiving greater camera trap research allocation partnering with the increased conservation effort. However, our findings further show that, even within the biomes, spatial disparities in research allocation in relation to the defaunation risk occur (Fig. 5B).

Terrestrial mammals and the threats to their persistence are unevenly distributed, and if camera trap research is primarily conducted to assess and monitor their defaunation risk, the distribution of species and the level of threat they face should guide research allocation (Wilson et al., 2016). However, we only found such a positive association in specific regions. For example, Southeast Asian tropical moist forests are both of high defaunation risk (Figure S5) and have received substantial camera trap research allocation, likely as a result of their rich biodiversity (Bai et al., 2021; Tilker et al., 2020), relative accessibility (compared to the Amazon or Congo), political stability, and economic growth. At the same time, these forests are also among the world's major defaunation hotspots due to high deforestation rates (Hansen et al., 2013; Hoang & Kanemoto, 2021; Potapov et al., 2017) and unsustainable levels of hunting (Benitez-Lopez et al., 2019; Gray et al., 2017, 2018; Tilker et al., 2019). The allocation of research in this region supports the research need to assess and monitor the consequences of these threats on terrestrial mammals. Our finding from Southeast Asia suggests that with additional and targeted efforts, similar high research allocation can be achieved in other areas where defaunation risk is high, charismatic species are present (Marshall et al., 2016) but camera trap research allocation is currently low.

The Amazon and Congo forest basins – are two biodiverse ecosystems facing unprecedented human alteration (Alamgir et al., 2017; Benitez-Lopez et al., 2019; Hansen et al., 2020; Kleinschroth et al., 2019; Lewis et al., 2015; Tyukavina et al., 2018) – received inadequate attention. Our findings indicate low levels of camera trap research in these regions despite their key role in climate regulation (Griscom et al., 2017; Mitchard, 2018; Steffen et al., 2018) and biodiversity conservation (Edwards et al., 2019; IPBES, 2019; Watson et al., 2018). Outside the tropics, we also observed a camera trap research shortfall (Fig. 5B) and a low probability of research allocation in Eastern Europe (Figs. 3C and 4O), despite this region's dominant biome, the temperate forest is facing a high defaunation risk (Figure S5). This again reflects a difference in country income across this biome (Fig. 4M). Camera research allocation was much lower in lower middle-income Ukraine, compared to the high probability of research allocation in the neighboring higher income countries of Poland, Slovakia, Hungary, and Romania (Figs. 3C and 4M). On the other hand, we also found some areas in the most camera trap researched biomes to have high camera trap research allocation but actually a low defaunation risk (Fig. 5B; Figure S5). These areas were mainly in the temperate forest biome in the USA, United Kingdom, China, Australia, and Japan where relative research intensity is often determined by national conservation priorities.

Conservation policy implications

To our knowledge, this is the first quantitative assessment of the degree to which camera trap research allocation matches global defaunation risk. Camera trap research allocation being lowest in low-income countries both globally and in all the four most researched biomes (Figs. 3 and 4) is unsurprising considering the financial and training investment needed for research – yet given how long this has been recognized (United Nations, 1992), progress remains disappointing. While economic growth may facilitate research allocation, this may be too late given the high global defaunation rates of terrestrial mammals (Allan et al., 2019; Benitez-Lopez et al., 2019; Ceballos et al., 2020; McCauley et al., 2015). It will be challenging to understand and track the impacts of anthropogenic activity on terrestrial mammal communities and ecosystem functioning if we do not take urgent action to expand and strengthen research in areas where defaunation risk is high, but research is lacking (Anderson, 2018; Kuhl et al., 2020; Moussy et al., 2022). Importantly, our findings complement ongoing calls for the strategic expansion of conservation initiatives particularly protected areas into specific regions that require additional protection (Allan et al., 2022; CBD, 2022; Ward et al., 2020; Williams et al., 2022). Increased research allocation in these areas will be key to generating *in-situ* primary data needed to monitor wildlife populations and assess protected area effectiveness (Cazalis et al., 2020; Geldmann et al., 2019; Laurance et al., 2012; Williams et al., 2022).

Because country income was the most important predictor for camera trap research allocation, we suggest that high-income countries fund research and conservation in countries where these are hampered by low income. In the absence of international aid, expanding research to the extent required to adequately monitor populations and assess conservation effectiveness may be difficult in low- and middle-income countries. Such countries are often homes for large numbers of underprotected species and underfunded protected areas but also are experiencing fast economic growth with associated negative impact on biodiversity (Giljum et al., 2022; Kleinschroth et al., 2019; Seto et al., 2012; Williams et al., 2020). Research extension may also be unlikely for underfunded biodiversity conservation budgets in low-income countries (Appleton et al., 2022; Coad et al., 2019; McCarthy et al., 2012). This is a particular concern given the existing trade-offs between research expansion and pressing socioeconomic and development priorities in the agriculture, education, health, security, and infrastructure sectors (Lewis et al., 2015).

The TEAM Network is one of the initiatives that show how high-income countries supported low- and middle-income countries to fill research gaps and provide an early warning system for biodiversity loss in tropical forest regions (Rovero & Ahumada, 2017). However, such initiatives need to be well rooted within the low-income countries with the active involvement of local scientists and organizations. Only the equal participation of local scientists and conservationists will guarantee that the research addresses the local conservation challenges to deliver the desired conservation outcomes, ensure capacity building and long-term sustainability of such research programs (Bockarie et al., 2018; Kuhl et al., 2020; Stefanoudis et al., 2021; Wilson et al., 2016).

We only assessed the location of camera trap research on terrestrial mammals regardless of its quality (i.e. camera trap grid design, number of camera trap sites, survey duration, etc.). However, we know how important research quality is for monitoring biodiversity (Ahumada et al., 2011; Anderson, 2018; Beaudrot et al., 2016; Bush et al., 2017; Kuhl et al., 2020). The heterogeneity in camera trap protocols and the associated lack of comparability may undermine the ability to track terrestrial mammal communities across biomes and inform conservation action to mitigate defaunation (Anderson, 2018; Bush et al., 2017; Kuhl et al., 2020). Future efforts should therefore not only extend camera trap research effort where it is currently limited but also ensure that quality camera trap designs are standardized to allow for adequate and comparable monitoring among locations, regions, ecosystems, and biomes. There are a number of guidelines and manuals available on how such a standardization could be achieved (Bush et al., 2017; Kuhl et al., 2020; Rovero & Ahumada, 2017). Certainly, more of these standardized initiatives (e.g. the TEAM Network) are needed to fill the shortfall in camera trap research allocation we report here and to track populations across time and space and thus monitor the risk of defaunation.

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Author Contributions

BM and AW conceived the project; BM designed the methodology and acquired and processed the data; BM conducted the data analysis with input from AW, SKS, JN, AP, and DS. BM led the writing of the manuscript with input from AW; All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest

The authors have no conflict of interest.

Data Availability Statement

The data and R code used for this study is available on GitHub here https://github.com/mweziMugerwa/mugerwa_2019_01_chapter1.git.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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