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Combining camera trap surveys and IUCN range maps to improve knowledge of species distributions

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Abstract

Reliable maps of species distributions are fundamental for biodiversity research and conservation. The International Union for Conservation of Nature (IUCN) range maps are widely recognized as authoritative representations of species' geographic limits, yet they might not always align with actual occurrence data. In recent area of habitat (AOH) maps, areas that are not habitat have been removed from IUCN ranges to reduce commission errors, but their concordance with actual species occurrence also remains untested. We tested concordance between occurrences recorded in camera trap surveys and predicted occurrences from the IUCN and AOH maps for 510 medium- to large-bodied mammalian species in 80 camera trap sampling areas. Across all areas, cameras detected only 39% of species expected to occur based on IUCN ranges and AOH maps; 85% of the IUCN only mismatches occurred within 200 km of range edges. Only 4% of species occurrences were detected by cameras outside IUCN ranges. The probability of mismatches between cameras and the IUCN range was significantly higher for smaller-bodied mammals and habitat specialists in the Neotropics and Indomalaya and in areas with shorter canopy forests. Our findings suggest that range and AOH maps rarely underrepresent areas where species occur, but they may more often overrepresent ranges by including areas where a species may be absent, particularly at range edges. We suggest that combining range maps with data from ground-based biodiversity sensors, such as camera traps, provides a richer knowledge base for conservation mapping and planning.

KEYWORDS
camera trap, IUCN, mammal distribution, mammal occurrence, range map, species distributions

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Combinación de censos con fototrampas y mapas de extensión de la UICN para incrementar el conocimiento sobre la distribución de las especies

Resumen: Los mapas confiables de la distribución de las especies son fundamentales para la investigación y conservación de la biodiversidad. Los mapas de distribución de la Unión Internacional para la Conservación de la Naturaleza (UICN) están reconocidos como representaciones de autoridad de los límites geográficos de las especies, aunque no siempre se alinean con los datos actuales de su presencia. En los mapas recientes de área de hábitat (ADH), las áreas que no son hábitat han sido eliminadas de la distribución de la UICN para reducir los errores de comisión, pero su concordancia con la presencia actual de las especies tampoco ha sido analizada. Analizamos la concordancia entre la presencia registrada por los censos de fototrampas y pronosticamos la presencia a partir de los mapas de la UICN y de ADH de 510 especies de mamíferos de talla mediana a grande en 80 áreas de muestreo de fototrampas. Las cámaras detectaron sólo el 39% de las especies esperadas con base en la distribución de la UICN y los mapas de ADH en todas las áreas; el 85% de las disparidades con la UICN ocurrieron dentro de los 200 km a partir del borde de la distribución. Sólo el 4% de la presencia de las especies fue detectada por las cámaras ubicadas fuera de la distribución de la UICN. La probabilidad de disparidad entre las cámaras y la UICN fue significativamente mayor para los mamíferos de talla pequeña y para los especialistas de hábitat en las regiones Neotropical e Indomalaya y en áreas con doseles forestales más bajos. Nuestros hallazgos sugieren que los mapas de distribución y ADH pocas veces subrepresentan las áreas con presencia de las especies, pero con frecuencia pueden sobrerrepresentar la distribución al incluir áreas en donde las especies pueden estar ausentes, en particular los bordes de la distribución. Sugerimos que la combinación de los mapas de distribución con los sensores de biodiversidad en tierra, como las fototrampas, proporciona una base más rica de conocimiento para el mapeo y la planeación de la conservación.

PALABRAS CLAVE

distribución de especies, distribución de mamíferos, fototrampas, mapa de distribución, presencia de mamíferos, UICN

摘要

可靠的物种分布图对生物多样性研究和保护至关重要。世界自然保护联盟(IUCN)的物种分布范围图被广泛认为是物种分布界限的权威表现, 但它们可能并不总是与实际出现数据一致。在最近的栖息地面积(AOH)图中, 非栖息地区域已从IUCN范围内移除, 以减少错误, 但它们与实际出现数据的一致性也未经测试。我们测试了全球80个红外相机调查区域中获取的510种中到大型兽类的出现数据与IUCN和AOH分布图之间的一致性。在所有区域中, 相机仅检测到基于IUCN范围和AOH图预期出现的39%的物种;85%的“仅IUCN类不匹配”发生在分布范围边缘的200公里内。仅有4%的物种被红外相机在IUCN分布范围外检测到。此种相机与IUCN范围之间的不匹配, 更易发于在新热带和印度马来亚以及在短冠层森林地区较小体型的哺乳动物和特化种。我们的发现表明, 分布范围和AOH地图很少低估物种出现的区域, 但它们可能高估物种的范围, 这种高估会包括物种缺失的区域, 尤其是在范围边缘。我们的研究显示, 将分布范围图与地面生物多样性传感器的数据相结合, 可为保护制图和规划提供更详实的知识基础。

结合红外相机调查和IUCN分布范围图以提升物种分布的认识

物种分布, 分布范围图, 世界自然保护联盟, 兽类分布, 红外相机, 兽类出现

INTRODUCTION

Understanding and predicting species distributions are fundamental components of biodiversity conservation and management. The assessment of species conservation status and subsequent development of conservation plans often depend on accurate range maps (Pimm et al., 2014; Zhu et al., 2021). Similarly, geographic priorities for conservation funding may be influenced by the use of range maps to delineate areas with high biodiversity or harboring threatened and endemic species

(Maxwell et al., 2020). For example, spatial patterns of the intensity of threats driving global biodiversity loss for terrestrial vertebrates have been identified based on range maps (Harfoot et al., 2021). Likewise, multiple iterations of global priority regions for mammalian conservation have been based on the known or predicted distribution of threatened species (Brum et al., 2017; Jenkins et al., 2013; Schipper et al., 2008). Inaccurate distribution maps could lead to erroneous conclusions regarding patterns of species richness and risk, thereby undermining the prioritization of conservation efforts in areas of high or threatened biodiversity (Hughes et al., 2021; Hurlbert & Jetz, 2007; Hurlbert & White, 2005) and the management of individual species (Garshelis et al., 2022; McShea et al., 2022).

Range maps were initially established to illustrate the geographic limits of species for taxonomic purposes but have been adapted for use in conservation assessment and macroecology (Marsh et al., 2022). In particular, range maps compiled by the International Union for Conservation of Nature (IUCN) are considered the gold standard for assessing species distributions and biodiversity trends (Brooks et al., 2019) and are frequently used to inform conservation efforts (Boitani et al., 2011). For example, these maps have been used to identify areas of high terrestrial diversity (Jenkins et al., 2013; Jung et al., 2021; Mason et al., 2020) and to assess the performance of the global protected area system in covering vertebrate geographic ranges (Pimm et al., 2018; Pouzols et al., 2014).

These maps are designed to represent the distributional limits of each species while minimizing omission errors (i.e., false absence of a species) at the cost of commission errors (i.e., false presence of a species). To create these maps, known occurrences of the species, expert knowledge of the taxon and its range, and information about habitat and elevation limits (IUCN, 2021) are used. However, comprehensive empirical data are limited for many species; therefore, range maps may be prone to bias and error (Drescher et al., 2013; Merow et al., 2017). The IUCN range maps may overestimate species distributions by including outdated or incorrect assessments of occurrence areas (Boitani et al., 2011; Rondinini et al., 2006). Range overestimation may result from range maps simply reflecting the extent of occurrence (EOO), defined as "the area contained within the shortest continuous imaginary boundary, which can be drawn to encompass all the known, inferred, or projected sites of present occurrence of a taxon, excluding cases of vagrancy" (IUCN, 2021). The EOO is often determined using a minimum convex polygon drawn around all known occurrence points (IUCN, 2021). Consequently, the resulting maps may be too liberal in extent because they include contiguous areas with similar landscapes that are uninhabited by the target species (Hurlbert & White, 2005). Alternatively, IUCN ranges may underestimate species distributions (Boitani et al., 2011; Rondinini et al., 2006). For instance, experts may conservatively restrict putative occurrences to areas with certain habitat characteristics, presumably, habitat where the species is known to have occurred rather than is suspected to occur, or disregard occurrences far beyond confirmed occurrence locations (Herkt et al., 2017; Schipper et al., 2008).

Therefore, reducing commission errors in range maps while minimizing omission errors is a critical step in accurately assessing species' distributions. One approach to achieving this is through the use of deductive modeling as it is applied, for example, in the area of habitat (AOH) approach. The AOH is defined as the habitat in the species' range and is derived by removing areas that are not habitat based on habitat and environmental information, such as land cover and elevation (Brooks et al., 2019; Lumbierres et al., 2022). Although AOH maps have recently become available for most mammals (Lumbierres et al., 2022), their large-scale validation has yet to be conducted (Ficetola et al., 2014; Rondinini et al., 2011). Furthermore, it remains unclear whether the AOH approach reduces commission and omission errors compared with the original IUCN range maps used to generate the AOH maps.

Previous researchers have compared IUCN range maps with species occurrence data derived from point sampling and found range maps are accurate for amphibians (Ficetola et al., 2014) but to often overestimate ranges for birds (Hurlbert & Jetz, 2007; Ramesh et al., 2017) and other taxa (Hughes, 2019; Hughes et al., 2021). However, inaccurate locality data can adversely affect the accuracy of IUCN maps (e.g., Hjarding et al., 2015). There is a need for IUCN mapping to take advantage of extensive high-quality occurrence data generated by the rapidly increasing use of ground-based biodiversity sensors, such as camera traps, which have become a prominent method for surveying medium- to large-bodied mammals (Ahumada et al., 2020; Hughes et al., 2021; Rondinini et al., 2011; Steenweg et al., 2017). Most studies of mammalian range maps have focused on underestimation, which can be quantified by documenting species occurrences outside their estimated range (Ficetola et al., 2014; Ramesh et al., 2017). By contrast, determining range overestimation is more difficult because confirming the absence of species is challenging and requires a large sampling effort (Dahal et al., 2021). For example, Li et al. (2020) used camera traps to document the likely absence of carnivores in several protected areas in China by surveying all major vegetation types over 3 years (> 5000 camera trap days in each protected area). Camera traps and other species-level biodiversity sensing technologies show great promise for faster assessment of potential over- or underestimation of species distributions (Kissling et al., 2018).

Estimation errors in species ranges may be associated with species ecology (Hughes, 2019; Jetz et al., 2008) and the extent of existing research on a given species (Ficetola et al., 2014; Martin et al., 2012). For example, small-bodied species can have limited ranges, and administrative boundaries may be used to delimit their range, especially in cases where ecological data are lacking. One might thus predict that the discrepancy between range maps and occurrence data may be higher for small-bodied than large-bodied species (Hughes, 2019). Additionally, the range maps more accurately capture the distributions of generalist species, which have wide ranges and broad habitats or environmental tolerances, compared to those of specialist taxa with narrow ranges (Wilson et al., 2004). Furthermore, the probability of detecting a given species during ecological field surveys can influence the understanding of its occurrence.

Whether species are detected by most survey methods, such as direct observations, tracks, interviewing locals, camera traps, can be affected by their conspicuousness. The conspicuousness of a species may be related not only to body mass (Burton, 2012), but also to diel activity patterns (Davies et al., 2020) and habitat affinities (Moore et al., 2021). For instance, small, nocturnal, and semiarboreal species are often more difficult to detect with camera traps. Detection probabilities are also affected by sampling effort and habitat type. For example, Kays et al. (2020a) found that at least 840 camera trap days were required to reliably detect most species in camera trap surveys, whereas Kolowski and Forrester (2017) found that squirrels were not easily detected by camera traps in structurally complex forests with high understory stem densities. The research effort expended on a species can also affect the quality of expert knowledge, distribution of survey effort, and access to occurrence data (Ficetola et al., 2014), thereby affecting the quality of the IUCN range map produced. Research effort may also show geographic and taxonomic biases. Charismatic species in wealthy counties, for example, tend to be overrepresented in the peer-reviewed literature (Donaldson et al., 2017; Martin et al., 2012; Meiri & Chapple, 2016; Wilson et al., 2016) and might, therefore, have more accurate range maps.

We examined the agreement between IUCN range maps and occurrences derived from camera trap surveys for medium- to large-bodied terrestrial mammals across 4 geographical realms with data from an extensive global data set (Chen et al., 2022). We quantified the extent of mismatches in species occurrences estimated from IUCN range maps and camera trap surveys to determine the potential for over- and underestimation of species ranges. To assess the potential of AOH maps in reducing the extent of mismatch between locality data and IUCN range maps, we repeated our analyses with the AOH maps and compared the results of the 2 tests. We assumed that species not detected by camera trap surveys at sites within their IUCN ranges and AOH maps represented potential cases of range overestimation, whereas species detected through camera trap surveys outside the IUCN range and AOH maps represented potential cases of range underestimation. Occupancy modeling is often applied to camera trap data to estimate imperfect detection (Burton et al., 2015), but we could not construct occupancy models for all of the camera trap surveys we included because raw-detection history data were not available for all surveys (details in Appendix S1). We, therefore, applied an occupancy modeling framework (Burton et al., 2011) in a test case to estimate the likelihood of a false absence for the rarest species in the lowest-effort survey included in our study. More generally, we tested the following a priori predictions regarding the agreement between IUCN range maps and camera trap detections: range maps and camera trap occurrences will be more similar for diurnal, large-bodied, ground-living habitat generalists and for species comprehensively and recently assessed by IUCN than for nocturnal, small, semiarboreal habitat specialists; range maps will have more overlap with camera trap occurrences in areas or biomes with extensive ecological research, such as the Nearctic realm and woodlands (Martin et al., 2012).

METHODS

Camera trap data

We used a previously assembled global data set of camera trap surveys (Chen et al., 2022) supplemented with an additional data set that included surveys from Southeast Asia (Mohd-Azlan et al., 2022) to extract a list of species detected through camera trap surveys from 2005 to 2018 (Chen et al., 2022) (Appendix S9). The surveys included data from projects run by coauthors and from publicly available databases (e.g., Wildlife Insights [Ahumada et al., 2020], eMammal [Kays et al., 2020b]). We excluded surveys with $<$ 400 camera days of total sampling effort and surveys that did not provide precise coordinates of sampling locations (Kays et al., 2020a; Tobler et al., 2008). We limited the scope of our inference to mammal species weighing $>$ 500 g based on the average body mass reported in the PanTHERIA database (Cusack et al., 2015; Jones et al., 2009). We thus excluded species $<$ 500 g and other species likely to be inconsistently detected with camera traps, including the following volant species and other rarely detected species (i.e., $<$ 2 detections per 10,000 trap days): bats (Chiroptera); golden moles and tenrecs (Afrosoricida); shrews, hedgehogs, and moles (Eulipotyphla); tree shrews (Scandentia); sengis (Macroscelidea); shrew opossums (Paucituberculata); and colugos (Dermoptera). In total, our data set included 80 camera trap surveys (collectively 747,731 camera trap days) conducted across 4 zoogeographic realms: Nearctic, Neotropical, Afrotropical, and Indomalaya (Figure 1 & Appendix S9). All occurrence records and species identifications were reviewed by the data collectors. Questionable records were removed from further analyses.

IUCN range map and AOH data

For each camera trap survey area, we extracted a list of medium- and large-bodied mammal species ($>$ 500 g) expected to occur according to the IUCN range maps. We used the spatial extent (e.g., shapefile) of a project if provided by the data source; otherwise, we created a minimal convex hull polygon with a 500-m area around the coordinates of all camera trap locations in each project. The IUCN range maps for all species were downloaded from the IUCN Red List website (https://www.iucnredlist.org/resources/spatial-data-download) in November 2020.

The IUCN classifies species ranges as extant or possibly extant. Following IUCN recommendations, we included only extant ranges because possibly extant ranges are areas with no record of the species but where species may possibly occur based on the distribution of potential habitat; therefore, they should not be considered when estimating the EOO (IUCN, 2021). Finally, to ensure comparability between the IUCN species list and the camera trap species list, we excluded species inconsistently detected by camera trap surveys by following the same species-filtering criteria described in the previous section. The AOH maps were obtained from Lumbierres et al. (2022)

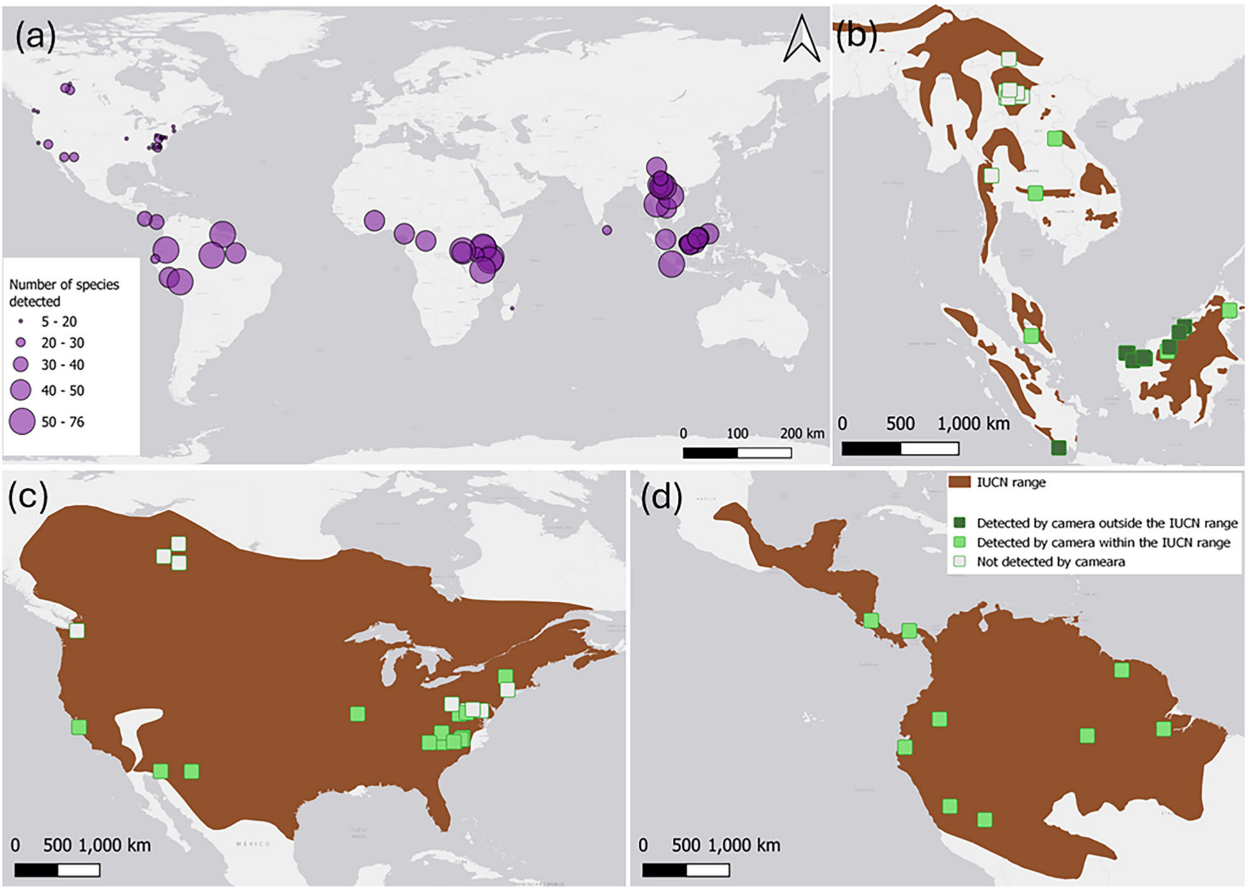

FIGURE 1 (a) Locations of 80 camera trap surveys and number of species detected, (b) marbled cat (*Pardofelis marmorata*) detections inside or outside its International Union for the Conservation of Nature (IUCN) range or not detected by cameras within the IUCN range, (c) striped skunk (*Mephitis mephitis*) not detected by some camera trap surveys within its IUCN range, and (d) common opossum (*Didelphis marsupialis*) detected by all camera trap surveys within its IUCN range.

and were produced from IUCN range maps (downloaded in May 2020) by subtracting areas that were not habitat, identified based on data on each species' associated habitat and elevation limits (Lumbierres et al., 2022). The AOH maps have a resolution of 100 m at the equator (Lumbierres et al., 2022). To elucidate the distinction between IUCN range maps and AOH, we examined the ratio between AOH and the IUCN range area for each species (as calculated previously in Lumbierres et al., 2022) (Appendix S13).

Explanatory variables for mismatch

We explored 4 classes of explanatory variables that we hypothesized would influence the mismatch between IUCN range maps and camera trap detections: species traits, camera trap sampling effort, research intensity, and habitat complexity (Table 1). For species traits, we focused on body mass (mean adult body mass in grams), habitat breadth, nocturnality, foraging stratum, and IUCN range area (square kilometers) (Appendix S14). Body mass was extracted from PanTHERIA (Jones et al., 2009), and the 3 niche traits were extracted from the Elton Traits database (Wilman et al., 2014). Body mass was included because it may influence detectability, and IUCN range area was included because wide-ranging species are often mapped with less detail; thus, both variables may lead to mismatches between the 2 methods. We included habitat breadth to test whether specialist or generalist species are more likely to have mismatches. Nocturnality and foraging stratum are related to species conspicuousness and can affect detection probability. Diurnal and ground-foraging species are more detectable and thus less likely to have mismatches. We included binary variables for nocturnality (1, nocturnal; 0, other) and foraging stratum (1, able to climb thus defined as semiarboreal; 0, restricted to terrestrial surfaces). We accounted for variation in camera trap sampling effort by modeling the total number of camera trap days per project. We incorporated the intensity of research effort (or knowledge production) that could inform IUCN range delineation for each species: frequency of IUCN Red List assessments per species, latest assessment year, IUCN extinction risk category (threatened species attract more conservation attention and research funding and, therefore, may be more extensively studied, resulting in them being mapped with higher precision), and biological realm where a camera trap survey was conducted (more

TABLE 1 Predictor variables included in the mixed-effects binomial models of mismatches between species International Union for the Conservation of Nature (IUCN) ranges and camera trap detections.

Variable	Description (data source)	Predictions
Species traits		
Body mass (g)	mean adult body mass of a species (Cusack et al., 2015; Jones et al., 2009)	large bodied species more detectable and thus more likely to have less mismatch
Foraging stratum	vertical strata where a species forages; categorical variable: G (1), species restricted to terrestrial surfaces; S (0), semiarboreal, species able to climb (Wilman et al., 2014); scansorial (climbing) and arboreal species	ground-foraging species more detectable, therefore, less mismatch
Habitat breadth	number of IUCN habitat types listed; range 1−35; large numbers indicate more generality for a species (Wilman et al., 2014)	specialists occupy fewer sites within their geographic range than generalists; range maps are coarse representations of species distribution and often include more inaccurate areas for specialists (more mismatch)
Range area (km^2)	range area of IUCN range map	wide-ranging species often mapped with much less detail and, therefore, more mismatches
Nocturnality	nocturnal (1), other (0) (Wilman et al., 2014)	nocturnal species less detectable and thus more likely to have inaccurate range maps and, therefore, more mismatch
Sampling effort or intensity of research		
Zoogeographical realm	zoogeographical realm where a camera trap survey was conducted; realms include Afrotropics, Indomalaya, Nearctic, Neotropics	species in realms with more ecological research (e.g., Nearctic) have less mismatch between IUCN range maps and camera trap detections than species in other realms
Camera sampling efforts	total camera days of a camera trap project	camera sampling efforts can increase the probability of species detection, therefore, there is less mismatch
IUCN year	year of latest IUCN assessments of a species	recent IUCN range maps have less mismatch between range maps and camera traps
IUCN frequency	total IUCN assessments of a species	species assessed more frequently have more accurate range map than species assessed less frequent, therefore, have less mismatch between IUCN range maps and camera traps
IUCN category	extinction risk of species assessed by IUCN; categories coded as integers: least concern (LC-1), near threatened (NT-2), vulnerable (VU-3), endangered (EN-4), and critically endangered (CR-5)	rare species with limited number of samples may be mapped to occupy a much larger range than it really occurred, and therefore, would have less mismatch between range maps and camera traps
Habitat		
Tree height (m)	forest canopy height (m) (Simard et al., 2011)	species in habitats with tall trees (structurally more complex environment) may not be easily detected and thus less likely to have accurate range maps

ecological research is conducted in some regions, e.g., Nearctic). Finally, species in different habitats (e.g., open area vs. closed forest) may vary in their probability of detection; therefore, we included mean canopy height (meters) as a coarse proxy for habitat type (Simard et al., 2011). All continuous variables were standardized to have a mean of 0 and a standard deviation of 1. Body mass data were transformed to log values.

Statistical analyses

We used binomial regression models to explore the relationship between occurrence mismatches and species traits, sampling effort, research intensity, and habitat complexity (Table 1). We developed a categorical match index to quantify mismatches between the 2 data sources. All species occurrences within each camera trap survey area were assigned to one of the following 3 categories (Figure 2): both, locations within the IUCN-determined range where species were detected by camera trap surveys; camera only, locations where species were detected by camera trap surveys outside their IUCN range, representing potential omission errors in the range delineation; and IUCN only: camera trap survey areas within a species IUCN range without detection of the species by the camera traps. These mismatches could be commission errors, although range maps are designed to indicate distribution limits but not necessarily fully occupied areas (as discussed above). Both were coded as 1 (no mismatch) and camera only and IUCN only were coded as 0. Separate models were run for each type of mismatch. We then compared camera trap occurrences with AOH maps in the same manner, with both, camera only, and AOH only categories.

To identify the factors explaining species detection with only 1 method (i.e., mismatch), we ran 2 sets of models. To test for potential underestimation of the IUCN range, we used

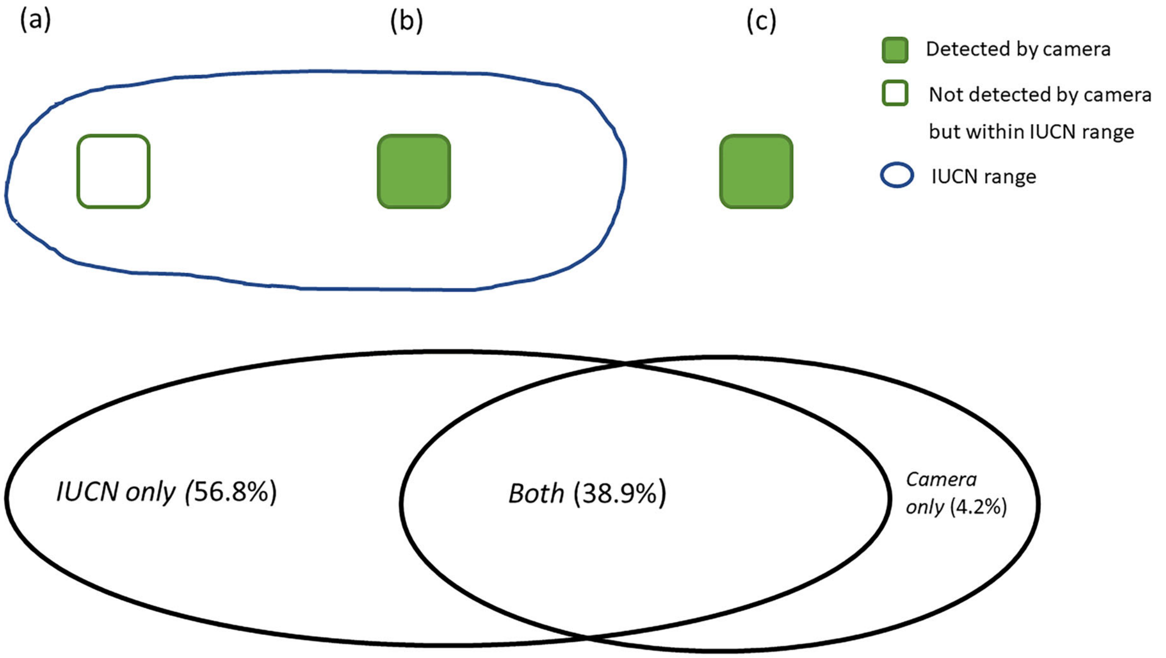

FIGURE 2 Conception of the 3 categories of species occurrences in each camera trap survey area (camera grid): (a) International Union for the Conservation of Nature (IUCN) range but not detected by cameras (IUCN only), (b) detected by cameras in IUCN range (both), and (c) detected by cameras outside IUCN range (camera only) (percentages, percentage of detections in each category across the 510 species from 80 projects).

response data with species occurrences representing camera only (0) and both (1). To test for potential range overestimation, we used IUCN only (0) and both (1). We calculated the minimum Euclidean distance from each camera trap to the nearest edge of a given species' range to quantify the number of sampling locations outside the IUCN range of that species. For each analysis, we compared the following 7 candidate models and a null model: species traits, sampling effort (for camera traps) or research intensity (for IUCN Red list assessment), model with habitat variable, models that included combinations of 2 of the abovementioned variables (models 4–6), and full model (Table 2). We included random intercepts in each model for the camera trap survey and species to account for potential nonindependence among observations of different species within the same camera trap survey and of the same species across different surveys, respectively.

We used Akaike's information criterion for small sample size (AIC_c) (Burnham & Anderson, 2002) to identify the most parsimonious candidate models that best explained the probability of species detection by only camera traps or IUCN range maps. Models with the lowest AIC_c value and highest AIC_c weight were identified as the best model, but all models with $\Delta\text{AIC} < 2$ were considered to have similar support. Furthermore, we used standardized regression coefficients and their 95% CIs to assess the direction, magnitude, and statistical significance of each explanatory variable included in the best model. The goodness of fit of the best model was estimated by Nakagawa's R^2 (Nakagawa et al., 2017). We repeated all statistical analyses with AOH-matching results. All statistical analyses were performed using the lme4 and MuMIn packages (Barton & Barton, 2015; Bates et al., 2015) in R 4.1.1 statistical software (R Core Team 2021). The replication data and code for binomial regression models can be obtained from (https://doi.org/10.5061/dryad.83bk3j9vp).

RESULTS

For the camera and IUCN range map comparison, of the 2966 total species × site occurrences, 1169 occurrences of 286 species (39%) were confirmed by camera detections within IUCN range (both), 107 occurrences of 65 species (4%) were detected by cameras outside IUCN range (camera only), and 1690 IUCN-assumed occurrences of 404 species (57%) were not confirmed by cameras (IUCN only) (Figure 2; Appendices S9 & S10). A comparison between camera trap data and AOH maps resulted in a total of 2875 species × site occurrences. Of these, 1144 occurrences of 283 species (40%) were in the both category, 132 occurrences of 72 species (4%) were camera only, and 1599 of 2875 (56%) were AOH only. Ninety-one IUCN only occurrences across 54 species were not validated by AOH and were subsequently excluded. Moreover, 32 camera occurrences that were within the IUCN range were not confirmed by AOH. Conversely, 7 camera only occurrences fell within the AOH, a result of the range correction for the crab-eating mongoose (*Urva urva*) because Lumbierres et al. (2022) factored in the possible extent area when creating the AOH for this species. The mean ratio between the areas covered by AOH and the IUCN range across all species was 0.80 (SD 0.20), indicating that, in general, AOH was not much smaller than the IUCN range.

TABLE 2 Model structure for candidate regression models of potential mismatch of International Union for the Conservation of Nature (IUCN) species' ranges and camera trap detections of species.*

Model	Body mass (g)	Foraging stratum	Habitat breadth	Nocturnality	Range area (km^2)	Realm	Camera days	IUCN year	IUCN frequency	IUCN category	Tree height (m)
Null											
Full	X	X	X	X	X	X	X	X	X	X	X
Species	X	X	X	X	X						
Sampling						X	X	X	X	X	
Habitat											X
Species + sampling	X	X	X	X	X	X	X	X	X	X	
Species + habitat	X	X	X	X	X						X
Sampling + habitat						X	X	X	X	X	X

*Cells with an x variable included in the model.

TABLE 3 Model selection results and models testing potential overestimation error of International Union for the Conservation of Nature mammal ranges based on detections from 80 camera trap studies.

Model	K	AIC$_c$[a]	ΔAIC$_c$[b]	AIC$_c$ weight[c]
Full	16	2791.02	0.00	0.82
Species traits + sampling	15	2794.07	3.04	0.18
Species traits	8	2864.27	73.25	0.00
Species traits + habitat	9	2865.71	74.68	0.00
Sampling + habitat	11	2874.08	83.05	0.00
Sampling	10	2876.13	85.10	0.00
Null	3	2959.58	168.56	0.00
Habitat	4	2961.52	170.50	0.00

[a] Akaike's information criterion.
[b] Difference in AIC$_c$ scores from the top-ranked model.
[c] Weight attributed to the model among all candidate models.

Potential range overestimation with IUCN only and AOH only occurrences

Using a test case of occupancy modeling for a rarely detected species, we estimated that the probability of false absence (p^{fa}) for an undetected species in our data set would be low (per entire survey $p^{fa} < 0.0072$ [Appendix S2]). IUCN only accounted for 57% of the mismatches in species occurrences between methods (Figure 2). Approximately one-quarter (105 of 404) of the species and one-third (426 of 1264) of the total occurrences with IUCN only records were classified as threatened (i.e., critically endangered, endangered, vulnerable). The mismatches between IUCN range maps and camera trap data were similar for the AOH maps; however, the AOH approach removed 91 IUCN-assumed occurrences in locations that were not habitat. The model selection and the estimated effects of factors explaining species detections by range maps and AOH maps were similar (Appendices S8–S10). About 85% of the IUCN only mismatches occurred within 200 km of range edges; 20% of them occurred directly on the edge (i.e., camera trap surveyed areas overlapping the border of the range) (Appendices S6 & S13). This pattern was consistent across all IUCN categories and for all species (Appendix S6).

The full model of the probability of correspondence between the IUCN range and AOH maps and camera trap detections with all explanatory variables had the lowest AIC$_c$ value (Table 3) and fit the data well (Nakagawa's conditional $R^2 = 0.65$). Consistent with our predictions, the probability of correspondence between IUCN range and camera trap detections (both) was positively associated with body mass ($\beta = 0.65$, 95% confidence intervals [CI] = 0.36–0.94) and habitat breadth ($\beta = 0.50$, 95% CI = 0.18–0.82) (Figure 3). The probability of detecting a species by camera within its IUCN range was 3 times greater for large-bodied species (20 kg) than for small-bodied species (0.5 kg) (Figures 3a & 4a). The regional discrepancy was strong. Compared with the Afrotropics, detection of species by cameras within IUCN ranges was significantly lower in the Indomalaya ($\beta = -1.49$, 95% CI = −2.32 to −0.66) and the

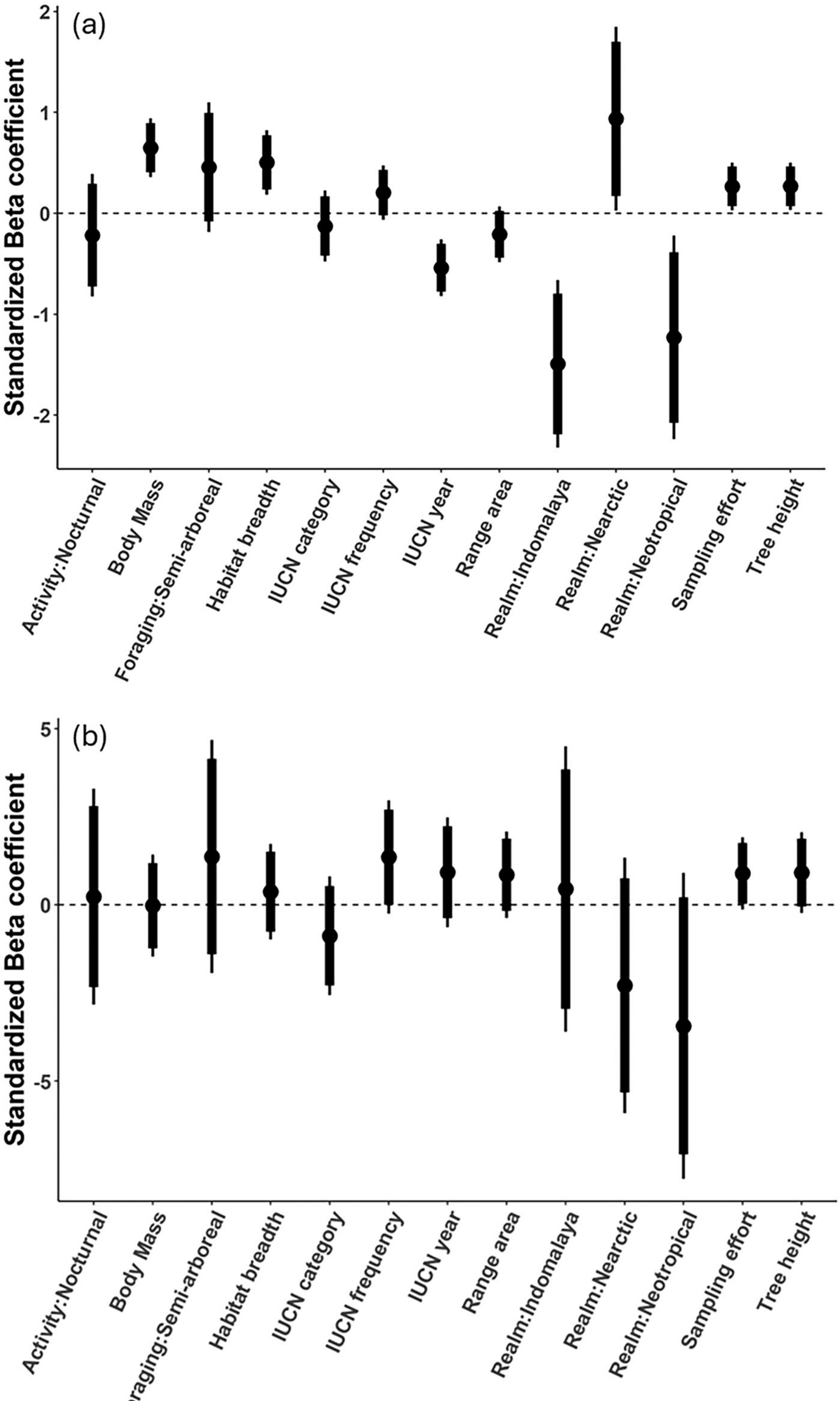

FIGURE 3 Regression coefficients (β) from the top-ranked model for factors associated with the probability of species detected by camera traps in species' International Union for the Conservation of Nature (IUCN) ranges (narrow bars, 95% confidence interval; wide bars, 90% confidence interval) based on (a) data from IUCN range (IUCN only) and overlaps between camera trap and IUCN ranges (both) and (b) data from areas exclusively detected by camera traps (outside IUCN range, camera only) and overlaps (both).

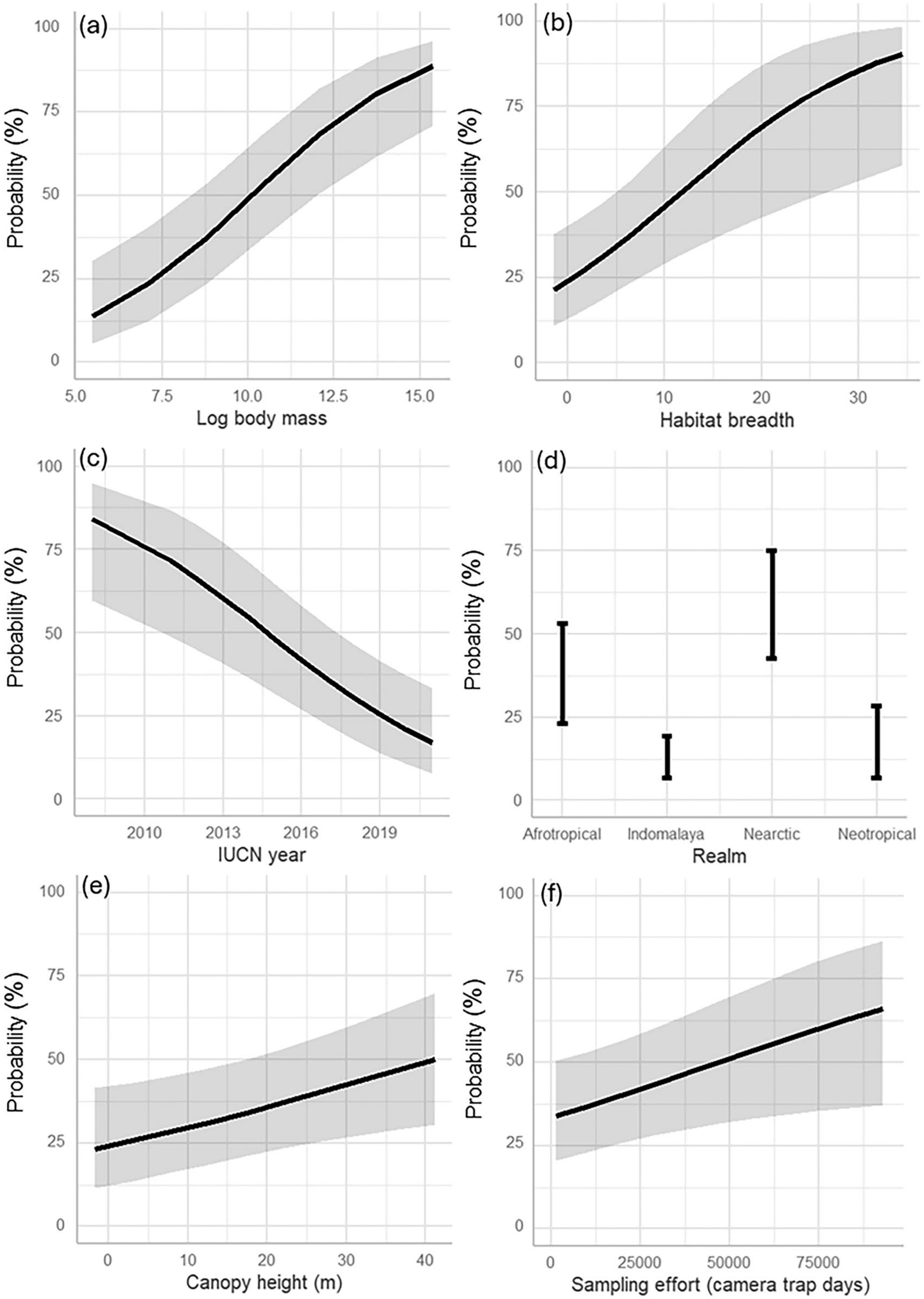

FIGURE 4 Relationships among model-predicted probabilities of species occurrences matching between camera trap detections and International Union for the Conservation of Nature (IUCN) ranges within camera survey areas. Predictions were made based on the best generalized linear model with IUCN only and both data (defined in legend of Figure 3) for the following variables: (a) species body mass, (b) species habitat breadth, (c) IUCN assessment year, (d) zoogeographical realm, (e) canopy height, and (f) sampling effort (camera trap days). Other variables were held at their means.

TABLE 4 Model selection results and models testing potential underestimation of International Union for the Conservation of Nature ranges of mammal species compared with mammal species' detections from 80 camera trap studies.

Model	K	$\mathrm{AIC_c}$[a]	$\Delta\mathrm{AIC_c}$[b]	$\mathrm{AIC_c}$ weight[c]
Full	16	520.30	0.00	0.54
Species traits + sampling	15	520.83	0.52	0.42
Species traits + habitat	9	526.96	6.66	0.02
Species traits	8	526.98	6.68	0.02
Sampling + habitat	11	540.77	20.47	0.00
Sampling	10	541.54	21.24	0.00
Habitat	4	547.24	26.94	0.00
Null	3	547.56	27.26	0.00

[a] Akaike's information criterion.

[b] Difference in $\mathrm{AIC_c}$ scores from the top-ranked model.

[c] Weight attributed to the model among all candidate models.

Neotropics ($\beta = -1.23$, 95% CI $= -2.24$ to -0.22), and significantly higher in the Nearctic ($\beta = 0.94$, 95% CI $= 0.03-1.85$) (Figures 3 & 4d). Species were more likely to occur in both IUCN range maps and camera surveys in areas with tall canopies ($\beta = 0.27$, 95% CI $= 0.04-0.50$). A mismatch was less likely when there was more sampling effort by cameras ($\beta = 0.27$, 95% CI $= 0.03-0.50$) (Figures 1b & 3). Contrary to our hypothesis, species with more recent IUCN assessments were more likely to have an IUCN only mismatch ($\beta = -0.54$, 95% CI $= -0.82$ to -0.26).

Potential range underestimation with camera only occurrences

In both comparisons (i.e., camera vs. IUCN range and camera vs. AOH maps), only 4% of mismatches were camera only (Figure 2). Of the 65 out-of-range species, 22 were threatened (critically endangered, endangered, vulnerable) and 44 were nonthreatened (near threat, least concern). Interestingly, 32 occurrence records shifted from both to camera only after removing areas that were not habitat based on AOH maps. However, the majority of these records (22 out of 32) were attributable to red fox (*Vulpes vulpes*) because the AOH map for this species did not include the extant and introduced region, resulting in all red fox occurrences in North America being categorized as camera only. After excluding the erroneous red fox records, the AOH comparison yielded only 10 more camera only occurrences than the IUCN comparison (Appendix S10). The modeling results for IUCN and AOH maps were also similar. The full model with all explanatory variables and the model with species traits plus sampling variables were favored (Table 4) but explained little overall variance ($R^2 < 0.1$). The 95% CIs for all parameter coefficients overlapped 0 (Figure 1b). Out of 108 camera only occurrences, three-quarters (75%) were detected within 300 km of the species range border (Appendix S4), see Appendix S7 for an example of out-of-range records of bearded pig [*Sus barbatus*].

Ten species occurred beyond 1000 km from the range border: crab-eating mongoose (*Herpestes urva*), eastern gray squirrel (*Sciurus carolinensis*), wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), Cape scrub hare (*Lepus saxatilis*), tapeti (*Sylvilagus brasiliensis*), Cape genet (*Genetta tigrina*), gray brocket (*Mazama gouazoubira*), Java mouse-deer (*Tragulus javanicus*), and Mondolfi's four-eyed opossum (*Philander mondolfii*). These mismatches were due to incomplete range representation, where, despite their known wide distributions within their respective regions, the extent of species range was not represented by IUCN range maps, such as for Eastern gray squirrel and crab-eating mongoose. Mismatches may also be due to species misidentification in camera images (Cape genet, Gray brocket, and Java mouse-deer), taxonomy change of the species (Cape scrub hare, tapeti), camera trap data input error (Mondolfi's four-eyed opossum), or the introduction of these species beyond their native range, such as for wild boar in North America (Lewis et al., 2019) and red deer in South America (Flueck, 2010). We reran models excluding these outlier species, but the results were qualitatively unchanged. Seven species were identified as occurring outside the AOH maps, namely, Cape hare (*Lepus capensis*), gerenuk (*Litocranius walleri*), Thomson's Gazelle (*Eudorcas thomsonii*), olive baboon (*Papio Anubis*), spectacled langur (*Trachypithecus obscurus*), masked palm civet (*Paguma larvata*), complex-toothed flying squirrel (*Trogopterus xanthipes*), in addition to those that were already identified as outside the IUCN range. Details of out-of-range records are in Appendix S10.

DISCUSSION

Comparison of data from camera trap surveys with IUCN range maps for medium- and large-bodied mammals revealed that few species were detected by cameras outside their IUCN range. By contrast, camera traps detected less than one-half of the species that were expected to occur in surveyed areas based on IUCN ranges. This large discrepancy could be due to a combination of range overestimation by the IUCN range maps and imperfect detection in camera trap surveys (false absences). However, we excluded species expected to be poorly detected by cameras from our analyses, and realistic detection probabilities for even rare species suggest that sampling effort was adequate in the camera trap surveys to lead to a low probability of false absences (Appendix S2). We, therefore, suspect that many of the observed mismatches reflected actual range overestimation. Recent instances of local extirpation could also cause range overestimation. For instance, buffalo, leopard, and giant forest hog are likely extirpated in Bwindi Impenetrable National Park, Uganda (Gorczynski et al., 2021; Rovero et al., 2020) and thus not detected by cameras even though their IUCN range overlaps the park. The temporal mismatches between camera traps and IUCN ranges were in both directions, with approximately one-half of species occurrences detected prior to IUCN assessments.

Despite our contention that the probability of false absence was low, camera trap sampling effort was positively associated with consistency between the range maps and camera traps in both overestimation and underestimation models. This emphasizes that adequate sampling effort is critical for estimating species richness for all empirical ecological surveys (Colwell et al., 2004), including camera trap surveys (Kays et al., 2020a). Although setting more cameras for longer periods can increase the probability of species detection, there are diminishing returns. Kays et al. (2020a) suggest that 840−2100 camera trap days are sufficient to obtain precise estimates of species richness (i.e., 3−5 weeks across 40−60 sites per camera trap array). The mean sampling effort for surveys in our study was 10,542 camera trap days (Appendix S9), 5 times greater than these minimum recommendations of Kays et al. (2020a). Additionally, the predicted relationship from our IUCN only model suggests that correspondence between IUCN range maps and camera traps would not be achieved until levels of sampling effort far exceed those determined in studies such as Kays et al.'s (2020a) (Figure 4f). Also, as indicated by our example estimation of probability of false absence (p^{fa}) for a hypothetical undetected species in the survey with lowest sampling effort (per entire survey effort $p^{\mathrm{fa}} < 0.0072$) (Appendix S2), camera trap surveys included in our analysis would likely have low probabilities of undetected species. Nevertheless, detecting very rare species with certainty can be difficult (Burton et al., 2011), and we cannot dismiss the possibility that some IUCN only mismatches could be due to cameras failing to detect a species that was present.

The IUCN range maps are designed to delineate the boundaries of a species' range rather than its internal distribution. As a result, it is expected that one will find areas within the range where the species is not detected due to an absence of habitat. This is particularly true for camera surveys located at the center of the species' range. In our analysis, however, we observed that the majority of species absences occurred at the fringes of their ranges (<200 km). This indicates that potential range overestimation might be widespread for many species. Broad-scale destruction of natural habitats, overexploitation of natural resources, competition with or predation by invasive non-native species, and climate change can contribute to recent range contraction. Local population extirpation can also lead to range overestimation (Faurby & Araújo, 2018; Pacifici et al., 2020; Li et al., 2020). This information is valuable for IUCN Red List assessments and underscores the importance of paying closer attention to the borders of ranges.

Our results showed that AOH maps derived from IUCN range maps for mammals also exhibited a high potential for commission errors. This is consistent with previous research on various taxa (Brooks et al., 2019; Hurlbert & White, 2005; Jetz et al., 2008; Rondinini et al., 2006; Vale et al., 2017). Even though AOH removes areas that are not habitat, camera trap studies were not randomly conducted within the range. Instead, we believe they were generally conducted in areas anticipated to contain diverse and abundant wildlife. Our comparison of camera detections with AOH maps confirms that mismatches within IUCN ranges were not limited to areas without habitat: 56% of occurrences were AOH only. The AOH was typically much smaller than the IUCN range map showed (Lumbierres et al., 2022); however, for the mammal species we analyzed, the mean ratio between the AOH and the area of the range was higher (0.8) than the mean across all species (0.4) analyzed by Lumbierres et al. (2022), indicating that much of the ranges for these mammals are considered to be in areas without habitat. This is consistent with the minimal difference we observed between the results of camera occurrences compared with ranges and AOHs. Nevertheless, AOH maps are also likely to vary in accuracy and may not account for anthropogenic factors that reduce suitability, such as habitat fragmentation or hunting. In general, AOH maps are a valuable tool that apply the geographic limits of species as a foundation to more accurately determine the areas genuinely inhabited by a species. Camera traps provide not only presence data, but also absence data with a high degree of confidence (Li et al., 2020). Therefore, combining camera trap surveys and species distribution mapping can be tremendously valuable in validating the accuracy of AOH maps (Dahal et al., 2021).

Our results illustrate the advantages of integrating camera trap data and range maps to detect biases and improve understanding of species distributions. Among the total 2973 occurrences, IUCN only and both accounted for approximately 57% and 40%, respectively, but the degree of mismatch varied between camera trap survey locations, which may reflect differences in research intensity among regions. As predicted, camera trap surveys in the Nearctic were more likely to detect species listed as extant on IUCN range maps compared with surveys in other realms, particularly the Neotropics and Indomalaya. Ecological field sites are disproportionately found in temperate deciduous woodlands (tall forests), and this geographic bias corresponds to gaps in ecological knowledge elsewhere (Martin et al., 2012; Nuñez et al., 2021). This suggests that camera trap surveys performed more poorly in the Neotropics, Indomalaya, and areas where forest canopy height was relatively lower, perhaps because mammal species in these areas may be less abundant. Consequently, more frequent assessments in these realms would greatly contribute to an improved understanding of species distributions and could increase consistency between range maps and ground-based sampling.

Species traits predicted the degree of potential range overestimation in the IUCN maps. Consistent with Jetz et al. (2008), generalists were more likely to be detected by both methods. An explanation is that specialists tend to occupy fewer sites within their geographic range than generalists (Grinnell, 1917). We similarly found niche breadth was positively associated with range map accuracy, as in Slatyer et al. (2013) Range maps thus tend to overestimate the geographical distribution of niche specialists. We found that range overestimation was positively related to body size but not to range area. Jetz et al. (2008) did not report a significant relationship with body size in birds, perhaps because mammals are in general more dispersal limited. Birds may, therefore, occupy more habitats than mammals of similar sizes because of their higher vagility. Likewise, Jetz et al. (2008) also reported a positive correlation between high habitat specificity and small range size in birds, but no such correlation was found in mammals. Foraging stratum and activity pattern were not significant predictors of the probability of species detected within the IUCN range, suggesting that camera traps can effectively detect ground and semiarboreal species during the day- or nighttime.

Few species were detected only in camera trap studies (4% of the total detections), and most out-of-range records were close to the IUCN range border. This indicates that IUCN range maps rarely underestimate the known distribution of most mid- to large-sized mammals. Although out-of-range records are infrequent, they provide valuable information, particularly for threatened species. A slight range extension for a species that is not threatened is unlikely to require a change in the IUCN Red List category or significantly alter the accuracy of species accounts. However, a legitimate range extension for a threatened species could significantly expand understanding of the species' distribution or habitat use, even resulting in a change in category. Such information is also beneficial for data-deficient species to help move them into data-sufficient categories. Additional studies are required to further investigate these out-of-range records, and increased sampling in these areas may be necessary.

Previous studies that used Global Biodiversity Information Facility (GBIF) occurrence data show that approximately 30% of mammal occurrences are outside their corresponding range map (Hughes, 2019; Hughes et al., 2021). This could be due to bias and taxonomic error in GBIF occurrences: over 25% of mammal occurrences were museum records (e.g., preserved specimens) that may no longer represent current ranges or were not properly curated and so contain taxonomic errors (e.g., Hjarding et al., 2015). Only approximately 10% represent recent observations (Wieczorek et al., 2012; Gbif.Org, 2018). Surprisingly, in our study, species more recently assessed by the IUCN were less likely to be detected by camera. We speculate that this is because recent IUCN assessments include a greater proportion of rare events not captured by camera trap surveys, such as recent local extirpation. Nonetheless, there could be temporal mismatches between camera survey years and the IUCN assessment year for some species.

A lack of comprehensive occurrence data can lead to inaccurate range maps influencing wildlife conservation efforts. To date, IUCN range maps are considered the most authoritative source for global conservation initiatives (Mason et al., 2020; Moran & Kanemoto, 2017) and site-scale conservation planning (Betts et al., 2020; Schipper et al., 2008). For instance, Mason et al. (2020) developed the index of transboundary conservation, which employs range maps of birds, mammals, and amphibians as a tool to identify country boundaries that require prioritization for animal conservation. Because IUCN range maps are derived from known species occurrence locations, IUCN species status is often determined from multiple data sources, including systematic surveys and expert opinion (Hayward, 2009). However, the quality of such data may vary substantially, depending on the level of individual expertise or survey method (Martin et al., 2012) and the frequency at which maps are updated. The IUCN assessments are typically updated every 5–20 years (except birds every 4 years) due to limited availability of occurrence data. Also, new occurrence records may not immediately be reflected in the assessment; consequently, expert maps can quickly become outdated (Merow et al., 2017). Camera traps, in contrast, can generate high-quality real-time data. Moreover, camera traps not only estimate the presence or absence of multiple species simultaneously, but also capture their abundance and behavior (Burton et al., 2022). The use of camera trap monitoring networks is rapidly expanding, with great potential to collect occurrence data across diverse habitat types. Furthermore, researchers may consider incorporating the use of other tools, such as species distribution modeling (Fourcade et al., 2013; Guisan & Thuiller, 2005), citizen science data (Ramesh et al., 2017), and other georeferenced data from GBIF (Hughes, 2019; Hughes et al., 2021), which can all help verify the accuracy of and, ultimately, improve IUCN range maps.

The use of IUCN range maps remains a central part of conservation planning, in part, because empirical occurrence data for many species are not always available. Camera trap data along with other new data sources such as acoustic and eDNA surveys can help fill this gap, and data-driven, automated, standardized alternatives for assessing and improving understanding of species distributions should be developed (Kissling et al., 2018). Promising alternatives include using habitat and elevation data to remove areas that are not habitat within species range and map species' AOH (Brooks et al., 2019); using species distribution models to combine species occurrences with ecogeographic information (Jetz et al., 2012); mapping not only simple binary predictions, but also species occurrence probabilities informed by rapidly accumulating camera trap data; and incorporating complementary data on important spatial heterogeneity within species ranges (Harris et al., 2022). New camera trap surveys could be targeted toward areas with greater uncertainty in predicted occurrence probabilities. Although it is challenging to harmonize and standardize biodiversity data from disparate sources, our results demonstrate that it is possible to compile and use camera trap data sets to yield insight into the distribution and conservation status of many larger-bodied mammal species (Ke & Luskin, 2019; Rostro-García et al., 2016). We echo previous calls for standardized camera trap data to facilitate data synthesis (Forrester et al., 2016), and we recommend open access to full data sets (e.g., Wildlife Insights) and specifically species occurrences (e.g., GBIF) whenever possible to improve wildlife science and conservation.

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SUPPORTING INFORMATION

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

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