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

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Keywords

species distributions; range map; IUCN; mammal distribution; camera trap; mammal occurrence

Article Impact Statement

Combining range maps with accumulating data from ground-based biodiversity sensors provides a knowledge base for conservation mapping

Abstract

Reliable maps of species distributions are fundamental for biodiversity research and conservation. The International Union for Conservation of Nature (IUCN) Red List range maps are widely recognized as authoritative representations of species' geographic limits, yet they might not always align with actual occurrence data. Recent Area of Habitat (AOH) maps remove unsuitable habitat from IUCN ranges to reduce commission errors, but remain untested. We tested concordance between occurrences from camera trap surveys and predicted occurrences from 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 or AOH maps, with 85% of the "IUCN-only" mismatches occurring within 200 kilometers of range edges. Only 4% of species occurrences were detected by cameras outside of IUCN ranges. The probability of mismatches between cameras and 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

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species occur, but 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 accumulating data from ground-based biodiversity sensors, such as camera traps, provides a richer knowledge base for conservation mapping and planning.

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 were 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 (Schipper et al. 2008; Jenkins et al. 2013; Brum et al. 2017). Consequently, inaccurate distribution maps could lead to erroneous conclusions regarding patterns of species richness and risk, thereby undermining attempts to prioritize conservation efforts in areas of high or threatened biodiversity (Hurlbert & White 2005; Hurlbert & Jetz 2007; Hughes et al. 2021) and for the management of individual species (Garshelis et al. 2022; McShea et al. 2022).

Range maps, polygons that demarcate the geographic distributions of species, 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) Red List 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; Mason et al. 2020; Jung et al. 2021) and to assess the performance of the global protected area system in covering vertebrate geographic ranges (Pouzols et al. 2014; Pimm et al. 2018).

These maps are designed to represent the distributional limits of each species while minimizing omission errors (i.e., the false absence of a species) at the cost of

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commission errors (i.e., the false presence of a species). To create these maps, known occurrences of the species are used in conjunction with expert knowledge of the taxon and its range, as well as information about habitat and elevation limits (IUCN 2021). 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). IUCN maps may overestimate species distributions by including outdated or incorrect assessments of occurrence areas (Rondinini et al. 2006; Boitani et al. 2011). Range over-estimation may result from range maps simply reflecting 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" (Jetz et al. 2008; 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 but that are uninhabited by the target species (Hurlbert & White 2005). Alternatively, IUCN maps may underestimate species distributions (Rondinini et al. 2006; Boitani et al. 2011), for instance when experts conservatively restrict putative occurrences to areas with certain habitat characteristics, presumably suitable habitat where the species is known rather than suspected to occur, or disregard occurrences lying far beyond confirmed localities (Schipper et al. 2008; Herkt et al. 2017).

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, such as the Area of Habitat (AOH) approach. The AOH is defined as the habitat within the species' range, which is derived by removing unsuitable habitat based on habitat and environmental information, such as land cover and elevation (Brooks et al. 2019; Lumbierres et al. 2022). While AOH maps have recently become available for most mammals (Lumbierres et al. 2022), their large-scale validation has yet to be conducted (Rondinini et al. 2011; Ficetola et al. 2014). Furthermore, it remains unclear whether the AOH approach reduces commission and omission errors compared to the original IUCN range maps used to generate the AOH maps.

Previous studies have compared IUCN range maps with species occurrence data derived from point sampling and found IUCN maps to be accurate for amphibians

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(Ficetola et al. 2014) but to often overestimate range for birds (Hurlbert & Jetz 2007; Ramesh et al. 2017) and other taxa (Hughes 2019; Hughes et al. 2021). However, it should be noted that inaccurate locality data can adversely affect the accuracy of IUCN maps (i.e. Hjarding et al. 2015). There is a need for IUCN mappings 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 (Rondinini et al. 2011; Steenweg et al. 2017; Ahumada et al. 2020; Hughes et al. 2021). Most studies of mammalian range maps have focused on underestimation, which can be quantified by documenting species occurrences outside of their estimated range (Ficetola et al. 2014; Ramesh et al. 2017). By contrast, determining range overestimation is more difficult as 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 three years, with > 5,000 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 (Jetz et al. 2008; Hughes 2019) and the extent of existing research on a given species (Martin et al. 2012; Ficetola et al. 2014). 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 otherwise lacking. We 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 distributions of wide-ranging generalist species with relatively broad habitats or environmental tolerances are captured more accurately by range maps than are those of narrow-ranging specialist taxa (Wilson et al. 2004). Furthermore, the known occurrence of a given species can be affected by the probability of detecting that species during ecological field surveys. Whether species are detected by most survey methods such as direct observations, tracks, interviewing locals, camera traps or other methods, can be affected by their conspicuousness. The conspicuousness of a species may be related not only to body mass (Burton 2012), but also diel activity patterns (Davies et al. 2020) and habitat affinities (Moore et al. 2021). For instance, small, nocturnal, and semi-arboreal species are often more difficult to detect by camera traps.

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Detection probabilities are also affected by sampling effort and habitat type. For example, Kays et al. (Kays et al. 2020a) found that at least 840 camera trap days were required to reliably detect most species in camera trap surveys, while Kolowski and Forrester (Kolowski & 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. Importantly, research effort may also show geographic and taxonomic biases. Charismatic species in wealthy counties, for example, tend to be overrepresented in peer-reviewed literature (Martin et al. 2012; Meiri & Chapple 2016; Wilson et al. 2016; Donaldson et al. 2017) and might therefore have more accurate range maps.

Here, we examined the agreement between IUCN range maps and occurrences derived from camera trap surveys for medium- to large-bodied terrestrial mammals across four geographical realms, using data from an extensive global dataset (Chen et al. 2022). We quantified the extent of mismatch 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 on reducing the extent of mismatch between locality data and IUCN range maps, we repeated our analysis with the AOH maps, and compared the results of the two tests. We assumed that species not detected by camera trap surveys at sites within their IUCN ranges/ AOH maps represented potential cases of range overestimation, whereas species detected through camera trap surveys outside the IUCN range/AOH maps represented potential cases of range underestimation. Occupancy modeling is one approach 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 included in our study because raw detection history data were not consistently available for all surveys (See Supplementary Methods for details). 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: 1) range maps and camera trap occurrences are more similar for diurnal, large-bodied, ground-living habitat generalists and for species comprehensively and recently assessed by IUCN than for nocturnal, smaller, semi-arboreal habitat specialists; 2) range maps have more overlap with camera trap

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occurrences in areas or biomes with extensive ecological research, such as the Nearctic realm and woodland habitats (Martin et al. 2012).

Materials and Methods

Camera trap data

We used a previously assembled global dataset of camera trap surveys (Chen et al. 2022), supplemented by an additional dataset including surveys from southeast Asia (Mohd-Azlan et al. 2022) to extract a list of species detected through camera trap surveys between 2005 and 2018 [Table S1 (Chen et al. 2022)]. The surveys included data from projects run by co-authors 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 or which did not provide precise coordinates of sampling locations (Tobler et al. 2008; Kays et al. 2020a). We limited the scope of our inference to mammal species weighing > 500 g based on average body mass reported in the PanTHERIA database (Jones et al. 2009; Cusack et al. 2015). We thus excluded species < 500 g, as well as 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 dataset included 80 camera trap surveys that collectively sampled 747,731 camera trap days across four zoogeographic realms: Nearctic, Neotropical, Afrotropical, and Indomalaya (Fig 1, Table S1). All occurrence records and species identification were reviewed by the data collector and questionable records were removed from further analysis.

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 buffer around the coordinates of all camera trap locations in each project. 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.

IUCN classifies species ranges as extant or possibly extant. Following IUCN recommendations, we only included extant ranges because possibly extant ranges are areas with no record of the species, but where species may possibly occur based

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on the distribution of potentially suitable habitat, and therefore should not be considered when estimating the EOO (IUCN 2021). Finally, to ensure comparability between the IUCN species list and camera trap species list, we excluded species inconsistently detected by camera trap surveys, following the same species filtering criteria described in the previous section. AOH maps were obtained from Lumbierres et al. (2022) and were produced from IUCN range maps (downloaded in May 2020) by subtracting unsuitable areas using 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)] (Table S5).

Explanatory variables for mismatch

We explored four classes of explanatory variables that we hypothesized would influence 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, g), habitat breadth, nocturnality, foraging stratum, and IUCN range area (km^2) (Table S6). Body mass was extracted from PanTHERIA (Jones et al. 2009) and the three niche traits were extracted from the Elton Traits database (Wilman et al. 2014). Body mass was included as it may influence detectability, and IUCN range area was included as wide-ranging species are often mapped with less detail, and thus both variables may lead to mismatches between the two 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, with diurnal and ground-foraging species being more detectable and thus less likely to have mismatches. We included binary variables for nocturnality (1 if nocturnal, 0 for other) and foraging stratum (1 if able to climb defined as semi-arboreal, 0 if restricted to terrestrial surfaces). We accounted for variation in camera trap sampling effort by modeling the total number of camera trap days per project. Additionally, we incorporated the intensity of research effort (or knowledge production) that could inform IUCN range delineation for each species, such as a) frequency of IUCN Red List assessments per species, b) latest assessment year, c) 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 d) biological realm where a camera trap survey was conducted (more ecological research is

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conducted in some regions, e.g., Nearctic). Finally, species in different habitats (e.g. open habitats vs closed forest) may vary in their probability of detection and we therefore included mean canopy height (m) 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 log-transformed.

Statistical Analysis

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 two data sources. All species occurrences within each camera trap survey area were assigned to one of the following three categories (Fig 2): 1) *Both*: locations where species were detected by camera trap surveys within the IUCN-determined range; 2) *Camera-only*: locations where species were detected by camera trap surveys outside their IUCN range, representing potential omission errors in the range delineation; 3) *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* was coded as 1 (no mismatch) and *Camera-only* and *IUCN-only* were coded as 0, with separate models 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 by only one method (i.e., mismatch), we ran two sets of models. To test for potential underestimation of IUCN range we used response data with species occurrences representing *Camera-only* (0) and *Both* (1), and to test for potential range overestimation we used *IUCN-only* (0) and *Both* (1). We calculated the minimum Euclidean distance from each camera trap location 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 seven candidate models and a null model: 1) species traits, 2) sampling effort (for camera traps) or research intensity (for IUCN Red list assessment), 3) habitat, 4)–6) models that included combinations of two of the abovementioned variables, and 7) full model (Table 2). We included random intercepts in each model for camera trap survey and species to account for potential

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non-independence 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 [AICc (Burnham & Anderson 2002)] to identify the most parsimonious candidate model(s) that best explained the probability of species detection by only camera traps or IUCN range maps. Models with the lowest AICc value and highest AICc weight were identified as the best model, but all models with ΔAIC < 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). Again, we repeated all statistical analysis with AOH matching results. All statistical analyses were performed using the *lme4* and *MuMIn* packages (Barton 2015; Bates et al. 2015) in R statistical software version 4.1.1 (R Core Team 2021).

Results

For the camera and IUCN range map comparison, of the 2,966 total species × site occurrences, 1,169 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 of IUCN range (*Camera-only*), and 1,690 IUCN-assumed occurrences of 404 species (57%) were not confirmed by cameras (*IUCN-only*; Fig 2; Table S1-2). A comparison between camera trap data and AOH maps resulted in a total of 2,875 species × site occurrences. Of these, 1,144 occurrences of 283 species (40%) were in the *Both* category, 132 occurrences of 72 species (4%) were *Camera-only,* and 1,599 of 2,875 (56%) were *AOH-only*. A total of 91 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 weren't confirmed by AOH. Conversely, 7 Camera-only occurrences fell within the AOH, a result of the range correction for the crab-eating mongoose, as 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 IUCN range across all species was 0.80 (standard deviation = 0.20) indicating that, in general, AOH was not much smaller than the IUCN range.

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Potential range overestimation (*IUCN-only/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 dataset would be low (per entire survey $p^{fa} < 0.0072$; Supplementary results). *IUCN-only* accounted for 57% of the mismatches in species occurrences between methods (Fig 2). Approximately one quarter (105/404) of the species and one third (426/1264) 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 that were located in unsuitable habitat. The model selection and the estimated effects of factors explaining species detections by range maps and AOH maps were similar (see Table S3,4 and Fig. S5b). About 85% of the 'IUCN-only' mismatches occurred within 200 kilometers of range edges, with 20% of them even occurring directly on the edge (i.e., camera trap surveyed areas overlapping the border of the range; Table S5, Fig. S2). This pattern was consistent across all IUCN categories and for all species (Fig S3).

The full model of the probability of correspondence between IUCN range/AOH maps and camera trap detections with all explanatory variables had the lowest Akaike's information corrected criterion (AICc) value (Table 4) and fit the data well (Nakagawa's conditional $R^2 = 0.65$). Consistent with our hypothesis, the probability of correspondence between IUCN range and camera trap detections (*Both*) was positively associated with body mass [β = 0.65, 95% confidence intervals (CI) = 0.36, 0.94] and habitat breadth (β = 0.50, 95% CI = 0.18, 0.82; Fig 3). The probability of detecting a species by camera within its IUCN range was three times greater for large-bodied species (20 kg) than for smaller-bodied species (0.5 kg; Fig. 3a, Fig 4a). Regional discrepancy was strong: compared with the Afrotropics, detection of species by cameras within IUCN ranges was significantly lower in the Indomalaya (β = -1.49, 95% CI =-2.32, -0.66) and the Neotropics (β = -1.23, 95% CI = -2.24, -0.22), and significantly higher in the Nearctic (β =0.94, 95% CI =0.03,1.85; Fig 3, Fig 4d). Species were more likely to occur in both IUCN range maps and camera surveys in areas with taller canopies (β = 0.27, 95% CI = 0.04, 0.50). A mismatch was less likely when there was more sampling effort by cameras (β = 0.27, 95% CI =0.03, 0.50; Fig 1b, Fig 3). Contrary to our hypothesis, species with more recent IUCN assessments were actually more likely to have an IUCN-only mismatch (β = -0.54, 95% CI = -0.82, -0.26).

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Potential range underestimation (*Camera-only* occurrences)

In both comparisons (i.e., Camera vs IUCN range and Camera vs AOH maps), only 4% of mismatches were *Camera-only* (Fig 2). Of the 65 out-of-range species, 22 were threatened (Critically Endangered, Endangered, Vulnerable) and 44 were non-threatened (Near Threat, Least Concern). Interestingly, 32 occurrence records shifted from *Both* to *Camera-only* after removing unsuitable habitat using AOH maps. However, the majority of these records (22 out of 32) were attributable to red fox (*Vulpes vulpes*), as the AOH map for this species did not include the Extant & Introduced region, resulting in all red fox occurrences in North America being categorized as Camera-only. After excluding these erroneous red fox records, the AOH comparison yielded only 10 more *Camera-only* occurrences than the IUCN comparison (Table S2). The modelling results for IUCN and AOH maps were also similar. The full model with all explanatory variables and model with species traits + sampling variables were favored by AICc (Table 3) but explained little overall variance ($R^2 < 0.1$). The 95% CIs for all parameter coefficients overlapped 0 (Fig 1b). Out of 108 *Camera-only* occurrences, three-quarters (75%) were detected within 300 km of the species range border (Fig S1, also see Fig S2, example of out-of-range records of bearded pig). Ten species occurred beyond 1,000 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 cases of mismatch were due to incomplete range representation where, despite known to have 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 re-ran models excluding these outlier species, but 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

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identified as outside the IUCN range. Details of out-of-range records are listed in Table S2.

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 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 maps, and imperfect detection in camera trap surveys (false absences). However, we excluded species expected to be poorly detected by cameras from our analysis, and realistic detection probabilities for even rare species suggest that sampling effort was adequate in the camera trap surveys to lead to low probability of false absences (Supplementary results). We therefore suspect that many of the observed mismatches reflect 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 (Rovero et al. 2020; Gorczynski et al. 2021) 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 half of the species occurrences being 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). While setting more cameras for longer periods can increase the probability of species detection, there are diminishing returns. Kays et al. (2020a) suggested that 840–2,100 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 (Table A.1), five times greater than these minimum recommendations by Kays et al. (2020a). Additionally, the predicted relationship from our IUCN-only model suggests that correspondence between IUCN range maps and camera traps

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would not be achieved until levels of sampling effort far exceed those determined in studies like Kays et al. (2020a) (Fig. 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 $p^{fa} < 0.0072$; Supplementary results) camera-trap surveys included in our analysis would likely have low probabilities of undetected species. Nevertheless, detecting very rare species with certainty can be difficulty (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.

We acknowledge that IUCN range maps are designed to delineate the boundaries of a species' range rather than its internal distribution. As a result, it is expected to find areas within the range where the species is not detected due to unsuitable habitat. This is particularly true for camera surveys located within 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 alien 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 Red List assessments and underscores the importance of paying closer attention to the borders of ranges.

Our study found that AOH maps derived from IUCN range maps for mammals, also exhibit high potential for commission errors. This is consistent with previous research on various taxa (Hurlbert & White 2005; Rondinini et al. 2006; Jetz et al. 2008; Vale et al. 2017; Brooks et al. 2019). Even though AOH removes unsuitable habitat, camera trap studies were not randomly placed 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 of unsuitable habitat: 56% of occurrences were AOH-only. AOH is typically much smaller than the range map; 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 in Lumbierres et al. (2022), indicating that much of the ranges for these

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mammals are considered to have suitable habitat. This is consistent with the minimal difference that 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 serve as a valuable tool, utilizing 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).

Furthermore, our study illustrates the advantages of integrating camera trap data and range maps to detect biases and improve our understanding of species distributions. Among the total 2,973 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 by IUCN range maps compared to 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 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 showed 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

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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 probability of species detected within IUCN range suggesting camera traps can effectively detect ground and semi-arboreal species during the day- or night-time.

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 Red List category or significantly alter the accuracy of species accounts. However, a legitimate range extension for a threatened species could significantly expand our understanding of the species' distribution or habitat use, even resulting in a change in Red List 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 found that approximately 30% of mammal occurrences were 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 and/or were not properly curated so contain taxonomic errors (e.g. Hjarding et al. 2015), with only approximately 10% representing 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 the recent IUCN assessments included a greater proportion of rare events not captured by camera trap surveys, such as recent local extirpation. We nonetheless acknowledge that there could be potential temporal

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mismatches between camera survey years and the IUCN assessment year for some species.

Lack of comprehensive occurrence data can lead to inaccurate range maps influencing wildlife conservation efforts. To date, IUCN maps are considered the most authoritative source for global conservation initiatives (Moran & Kanemoto 2017; Mason et al. 2020) and site-scale conservation planning (Schipper et al. 2008; Betts et al. 2020). 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. 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 (Guisan & Thuiller 2005; Fourcade et al. 2013), 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: 1) using habitat and elevation data to remove unsuitable habitat within species range and map species'

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Area of Habitat (AOH) (Brooks et al. 2019); 2) using species distribution models to combine species occurrences with eco-geographic information (Jetz et al. 2012); 3) mapping not only simple binary predictions but estimates of species occurrence probabilities informed by rapidly accumulating camera trap data; 4) incorporating complementary data on important spatial heterogeneity within species ranges (Harris et al. 2022). New camera trap surveys could be targeted towards areas with greater uncertainty in predicted occurrence probabilities. Although it is challenging to harmonize and standardize biodiversity data from disparate sources, our study demonstrates that it is possible to compile and use camera trap datasets to yield insight into the distribution and conservation status of many larger bodied mammal species (Rostro-García et al. 2016; Ke & Luskin 2019). We echo previous calls for standardized camera trap data to facilitate data synthesis (Forrester et al. 2016), and we recommend open access to full datasets (e.g. Wildlife Insights) and specifically species occurrences (e.g. GBIF) whenever possible to facilitate improved wildlife science and conservation.

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Data and materials availability

Camera trap data obtained from eMammal (https://emammal.si.edu), TEAM (https://www.conservation.org/projects/team-network), now Wildlife Insights (https://www.wildlifeinsights.org/). Range maps obtained from IUCN Red list (https://www.iucnredlist.org). The replication data and code for binomial regression

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models can be obtained from (https://datadryad.org/stash/share/AT-a4Yb9R990eO-l2GWO_iS5UVygZndgQXAo-dHVdT0).

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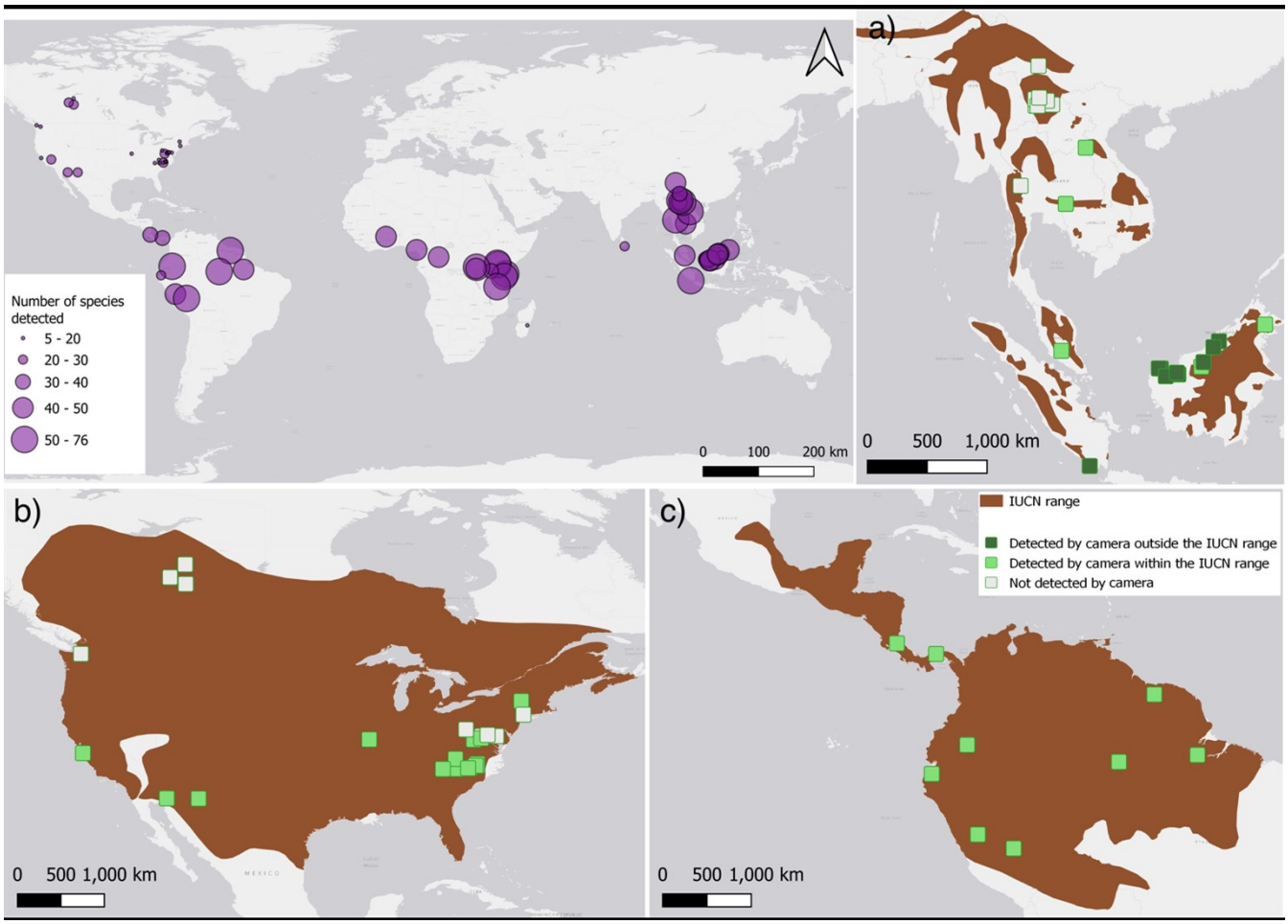


Fig 1. Locations of 80 camera trap surveys and examples of match or mismatch scenarios for three mammalian species from different continents. a) Marbled cat (*Pardofelis marmorata*), detected by camera trap surveys within or outside its IUCN range, or not detected by camera within the IUCN range; b) striped skunk (*Mephitis mephitis*), not detected by some camera traps within the IUCN range; and c) common opossum (*Didelphis marsupialis*), detected by all camera trap surveys that were within its IUCN range.

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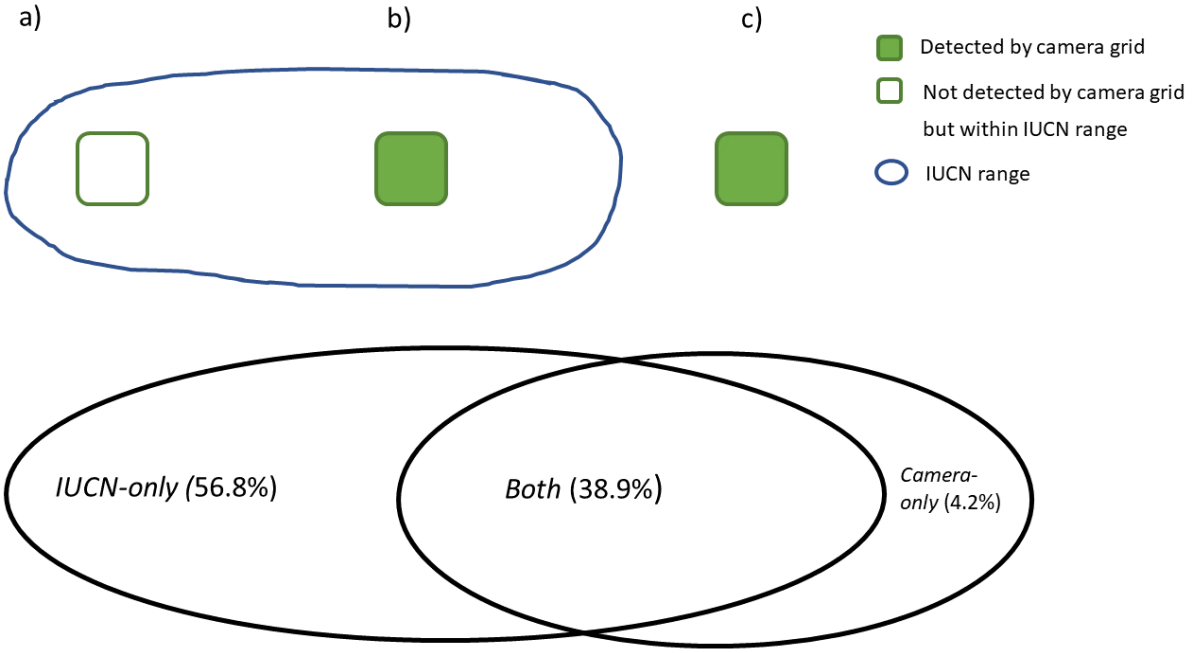


Fig 2. Above: Conceptual diagram showing the three categories of species occurrences within each camera trap survey area (camera grid). a) *IUCN-only*, b) *Both,* and c) *Camera-only.* Below: observed percentages in each category across the 510 species from 80 projects.

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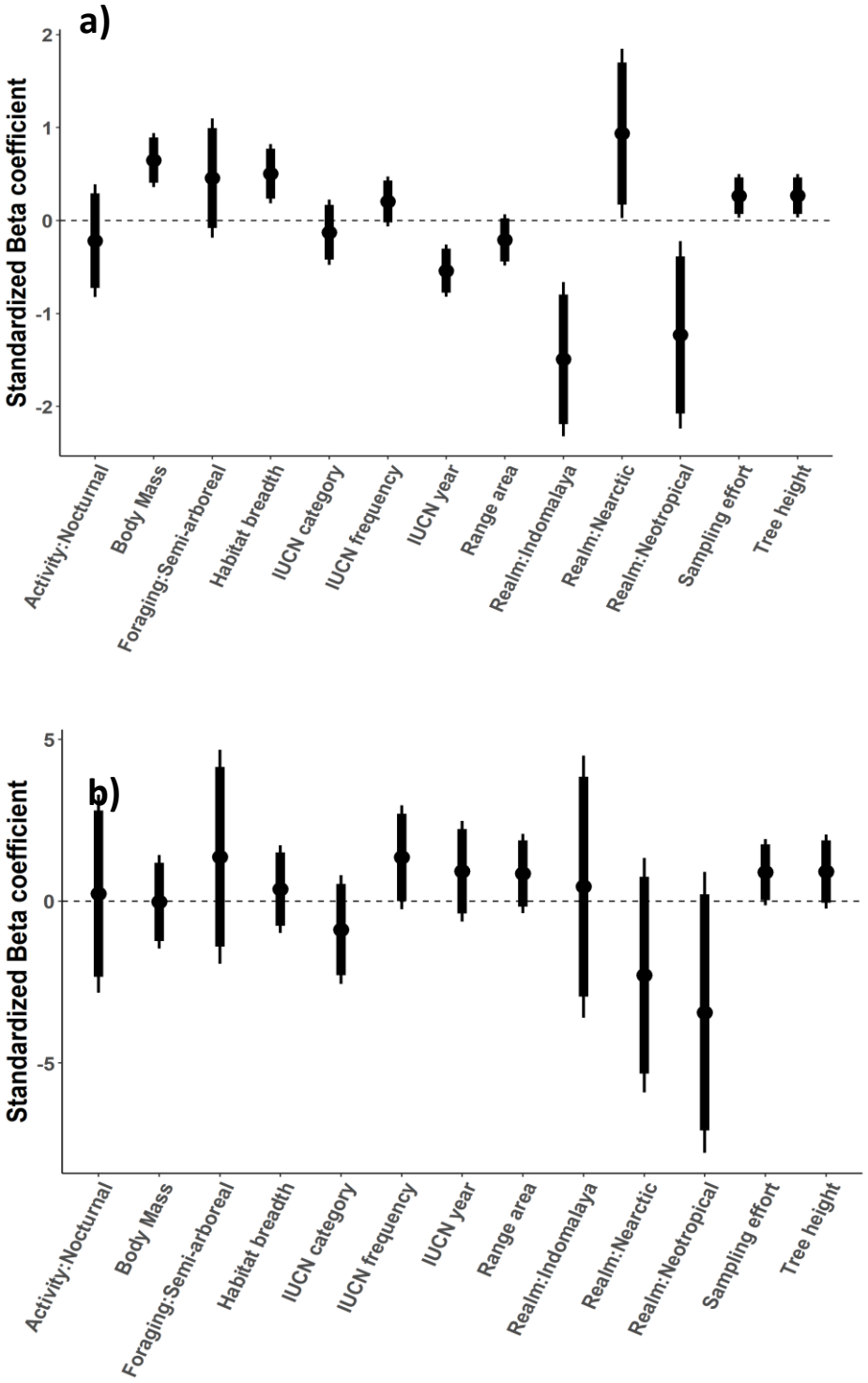


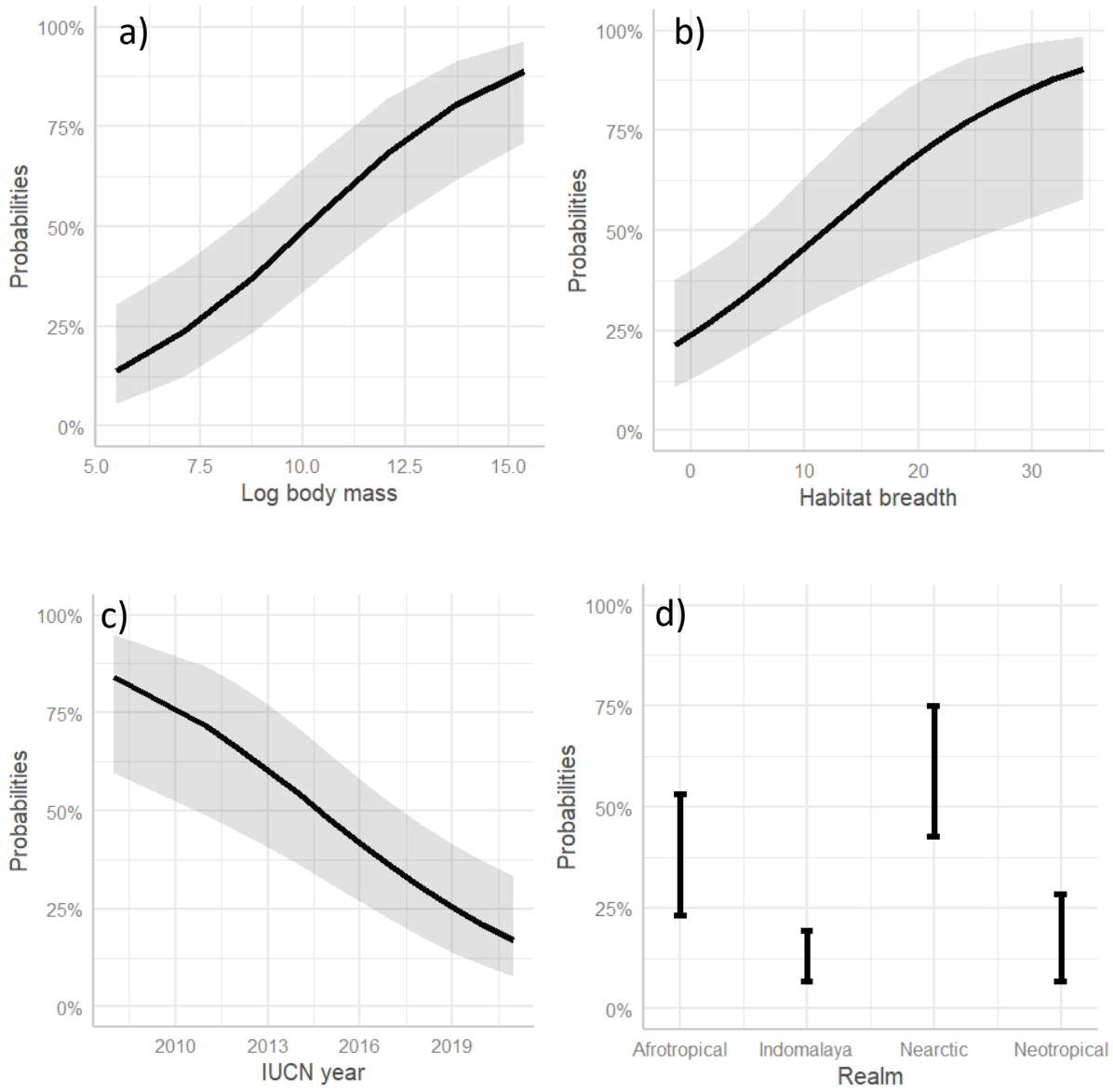
Fig 3. Regression coefficients (β) from the top-ranked model for factors associated with the probability of species detected by both camera trap and IUCN range maps

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(vertical line within bars: mean; narrow bars: 95% confidence interval, CI; wide bars: 90% CI) using **a)** *IUCN-only* and *Both* data, **b)** *Camera-only* and *Both* data.



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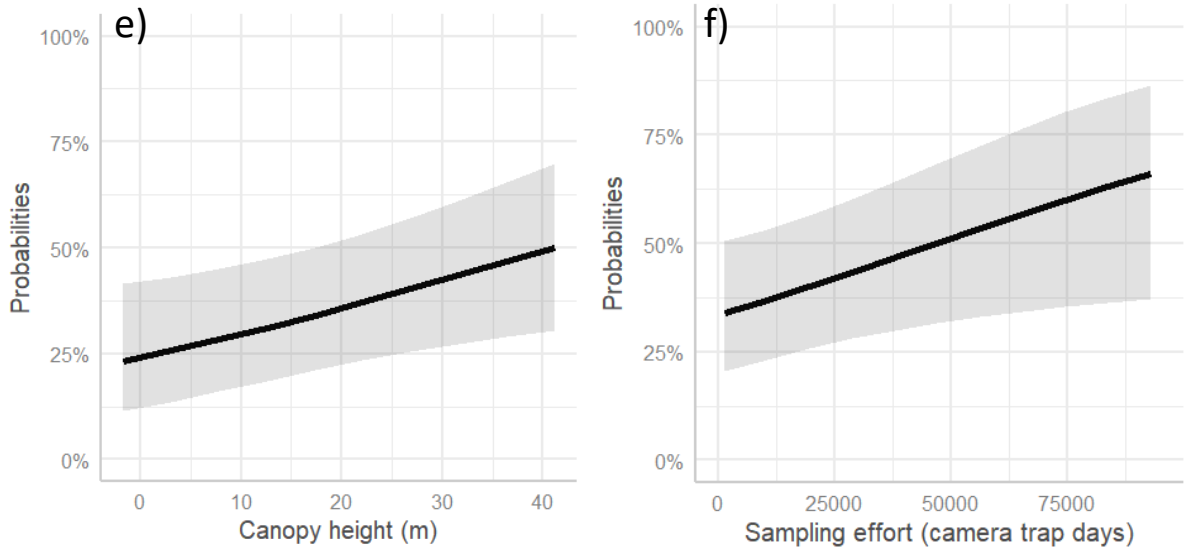


Fig 4. Relationships among model-predicted probabilities of species occurrences matching between camera trap detections and IUCN range maps within camera survey areas. Predictions were made based on the best generalized linear model using *IUCN-only* and *Both* data for the following variables while other variables were held at their means **a)** species body mass, **b)** species habitat breadth, **c)** IUCN assessment year, and **d)** zoogeographical realm **e)** canopy height **f)** Sampling effort (camera trap days).

Table 1. Predictor variables included in the mixed-effects binomial models to explain mismatches between IUCN range maps and camera trap surveys.

Variable	Description & data source	Predictions
Species traits		
Body mass (g)	Mean adult body mass of a species (g) (Cusack et al., 2015; Jones et al., 2009).	Larger bodied species are more detectable, and thus more likely to have less mismatch.
Foraging stratum	Vertical strata where a species forages. Categorical variable: G (1)	Ground-foraging species are more detectable therefore have less

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	– species restricted to terrestrial surfaces, Semi-Ar (0) - Semi-arboreal: species are able to climb (Wilman et al. 2014). Scansorial (climbing) and arboreal species.	mismatch.
Habitat breadth	The number of IUCN habitats listed as suitable. Ranging from 1–35, larger numbers indicate more generality for one species (Wilman et al. 2014).	Specialists would 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 are often mapped with much less detail and therefore more mismatches between two methods.
Nocturnality	Whether a species is active primarily at night: nocturnal (1), other (0); (Wilman et al. 2014).	Nocturnal species are less detectable and thus more likely to have inaccurate range maps (i.e., more mismatch)
Sampling effort or intensity of research		
Zoogeographical realm	The zoogeographical realm where a camera trap survey was conducted. Realms include Afrotropics, Indomalaya, Nearctic, and Neotropics.	Species in realms with more ecological research (e.g., Nearctic) would have less mismatches between range maps camera traps than species in other realms.
Camera sampling efforts	The total camera days of a	Camera sampling efforts

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	camera trap project	can increase the probability of species detection by camera trap led to less mismatch.
IUCN year	Year of latest IUCN assessments of a species	Recent IUCN range maps have less mismatches between range maps camera traps.
IUCN frequency	Total IUCN assessments of a species	Species assessed more frequently would have more accurate range map than species assessed less frequent therefore have less mismatches between range maps camera traps.
IUCN category	The extinction risk of species assessed by IUCN Red List. Categories were 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 occupies a much larger range than it really occurred therefore would have less mismatches between range maps camera traps.
Habitat		
Tree height (m)	Forest canopy height (m);(Simard et al. 2011)	Species live in habitats with higher trees (more structurally complex environment) may not easily detected and thus less likely to have accurate range maps.

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Table 2. Model structure for candidate regression models explaining potential mismatch of range maps. Cells with an "x" indicate the variables that were included in each model.

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

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Table 3. Model selection results and models testing potential underestimation of IUCN range maps for mammals compared with detections from 80 camera trap studies (*Camera-only* models). Bold values indicate the variables that best explained underestimation. ΔAICc indicates the difference in AICc scores from the top-ranked model and AICc weight is the weight attributed to that model among all candidate models.

Model	K	AICc	ΔAICc	AICc weight
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

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Table 4. **Model selection results and models testing potential overestimation error of mammal range maps from 80 camera trap studies (IUCN-only models).** Bold values indicate the variables that best explained overestimation. ΔAICc indicates the difference in AICc scores from the top-ranked model and AICc weight is the weight attributed to that model among all candidate models.

Model	K	AICc	ΔAICc	AICc weight
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

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