

Mapping hunting probability across the tropics in space and time

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18 **Abstract**

19 Hunting is a major driver of global species extinctions, yet the spatial footprint and
20 temporal trends of this threat are lacking at the global scale, limiting our ability to achieve
21 international policy targets. Here, we present standardized global maps of hunting
22 probability across the tropics, based on a machine learning algorithm trained on 2,463
23 hunted and non-hunted tropical sites, spatially and temporally matched to ecological and
24 socio-economic predictors. We estimate the spatial footprint of hunting extends across
25 the entire pantropical zone, with distinct hotspots of high predicted hunting occurrence
26 probability in the Indomalayan realm (e.g., China, Sri Lanka, Western India), the Brazilian
27 Atlantic Forest, and parts of West Africa. Refuges from hunting persist in remote areas of
28 interior Borneo, Papua New Guinea, Central Africa, and the western Amazon. Enhanced
29 human accessibility has facilitated the geographic expansion of hunting from 2000-2015,
30 most notably in regions historically considered undisturbed and remote such as the
31 Amazon basin, and in areas already facing high pressure such as China and Indonesia.
32 Spatio-temporal dynamics also varied among realms. Our standardized spatio-temporal
33 assessment provides a blueprint to inform conservation, supporting targeted
34 management actions and informed policy interventions to mitigate hunting impacts.

35

36 **Main text**

37 From agoutis and songbirds to hornbills and rhinos, humans have hunted wildlife for
38 millennia^{1,2}. Nowadays, however, unsustainable hunting for consumption and trade of
39 wild animals represents a major extinction threat to terrestrial vertebrates³⁻⁵. Wild
40 vertebrates are harvested for a variety of reasons, both legally and illegally. These include
41 direct consumption as food⁶, the production of traditional medicine, tools, or ornaments,
42 as well as for the pet trade^{7,8}. Hunting impacts thousands of bird and mammal species
43 globally, especially for trading purposes⁸, leading to significant declines for some species
44⁹, acting as a primary driver of extinction^{8,10}, and potentially impacting tree regeneration
45 in ways that affect forest carbon storage capacity¹¹. Additionally, vertebrate species can
46 be non-randomly harvested, with specific traits such as body size, colorful plumage, or
47 body parts with ornamental uses making them more likely targeted than others^{8,12-15},
48 leading to increased endangerment of phylogenetically clustered branches of the tree of
49 life⁸.

50

51 Data on the extent, patterns, and trends of where hunting occurs, and its intensity are
52 essential for guiding global and national conservation and sustainable development
53 priorities. Unlike most other anthropogenic threats such as logging, urbanization,
54 agriculture, and fire events¹⁶⁻¹⁸, which can be effectively monitored through remote
55 sensing^{19,20}, hunting remains challenging to be detected, due to its cryptic and often
56 clandestine nature. Consequently, hunting represents only a small fraction (less than 5%)
57 of the available spatially explicit datasets on global threats²¹. Furthermore, the cryptic
58 impacts of hunting contribute to the phenomenon of 'empty forests'²² or 'half-empty

forests' ²³, terms that describe forest ecosystems that appear structurally intact but have experienced significant wildlife declines due to unsustainable harvesting ²⁴.

To address this need, several approaches have been developed, including mechanistic models that predict hunting pressure (from low to high) ^{5,25}, as well as correlative models that estimate biomass offtake ^{26,27,28} or hunting-induced declines in species abundance ^{29,30}. Alternative approaches map the probability of species being threatened by hunting within grid cells, based on IUCN species' geographic ranges and qualitative data from threat assessments ³¹. Collectively, these methodologies have significantly advanced global mapping efforts, enhancing our understanding of the spatial footprint of hunting across the tropics. Yet, the existing approaches have several shortcomings that hamper our ability to fully gauge the pervasiveness of hunting across the globe, as well as its implementation in cumulative threat maps or its reliability to inform international policy processes. For example, mechanistic models produce a unitless hunting pressure index that lacks external validation and calibration, limiting their practical use. In turn, current correlative models, which focus on complex continuous outcomes such as changes in abundance or biomass offtake, rely on data that are difficult to obtain ²⁶⁻³⁰. As a result, they are often biased due to restricted spatial and taxonomic coverage, resulting in moderate predictive performance at global scale (but see ^{27,28} for local studies). While these models can still provide valuable insights, they often come with high uncertainty especially at finer spatial scales. Further, because some of these correlative models rely on species distribution data, their resulting maps are difficult to integrate with other, biodiversity-agnostic, spatial layers of human pressure (e.g., Anthromes ³², Forest Landscape Integrity Index ²⁰, Global Human Modification ³³, Human Footprint ¹⁹, Low

Impact Areas ³⁴). Combining biodiversity information *a posteriori*, such as species distribution or richness, with spatial layers of individual threats (i.e., mapped independently from biodiversity) enables a wide range of follow-up analyses. It allows the construction of spatially explicit vulnerability estimates that can provide valuable insights for local-scale biodiversity conservation (e.g., ³⁵). Threat maps based on the distribution of species threatened by hunting according to the IUCN Red List (e.g., ^{31,36}) also suffer from well-known limitations inherent to the assessment process itself ^{37–40} as well as from the lack of integration of spatial ecological and socio-economic proxies of hunting activity. These include inconsistent evaluation criteria among species, low spatial accuracy at finer scales, and reliance on generalized range-wide assessments rather than spatially explicit threat quantification. Consequently, this approach inadequately captures local variability and complexity in hunting processes, which depend on socio-economic, cultural, and ecological contexts at both local and regional scales (see, for example, ⁴¹ for context-dependent patterns of wild animal hunting in African tropical forests).

To address these limitations, we conducted a comprehensive literature review and compiled an extensive georeferenced dataset comprising 2,463 sites classified as either hunted or non-hunted across tropical regions (Fig. 1; *Supplementary Information* Fig. S1). Hunted sites correspond to locations where hunting activity is reported to occur, irrespective of form or intensity (e.g. legal or illegal, sustainable or unsustainable, using firearms or snares), as documented in the original studies. Non-hunted sites were used as control locations and correspond to areas described by the authors as not known to be hunted and for which no evidence of hunting activity was reported, representing true

absences of hunting occurrence based on scientific evidence Each site was spatially and temporally matched with a set of socio-economic and ecological predictors commonly recognized as major drivers of hunting at large spatial scales (Table 1). Using these spatially and temporally aligned datasets, we trained supervised binary classifiers (random forests) to estimate the probability of hunting occurrence across time periods. Predictions, bounded between 0 and 1, define our Hunting Probability (HP) score at 1 × 1 km resolution. Expressing hunting as a continuous, standardized probability, yields an objective, directly comparable metric of potential hunting exposure across the tropics, which can be swiftly integrated with other layers of human pressure (e.g. Global Human Modification). We focused our analyses on global HP mapping for the years 2000 and 2015, corresponding to periods for which most predictor layers were available at the subsequent time periods. This temporal framework, previously applied to forest fragmentation ²⁰, enables the detection of global, regional and local trends in hunting exposure. The HP spatial layers are intended as a flexible analysis tool rather than a standalone prioritization product: combined with complementary biodiversity layers (species distributions, abundance, richness or vulnerability) matched to the scale and objective of each application, they offer a standardized, spatially explicit basis for targeting conservation interventions from regional to subnational scales.

Results

HP modeling

Random forests predicting HP performed strongly (all $\pm$ values are mean $\pm$ SD across cross-validation folds unless stated otherwise; AUC = 0.90 ± 0.016 ; MCC = 0.58 ± 0.031 ;

accuracy = 0.81 ± 0.016 ; *Supplementary Information*, Fig. S2–S6). Six socio-economic and ecological predictors drove HP (Fig. 2). Distance to settlement dominated (mean|SHAP| = 0.085 ± 0.064), with HP rising sharply within 25 km (Fig. 2A & 2B). Forest cover within 20 km ranked second (0.057 ± 0.035), peaking at ~75% cover, followed by HDI (0.053 ± 0.042), which showed a non-linear U-shape. Livestock biomass and NPP had moderate effects; remaining predictors contributed little (Fig. 2A; *Supplementary Information* Fig. S7–S8). Spatial autocorrelation was negligible (Moran's I = 0.017–0.030; *Supplementary Information* Fig. S9). Both the MESS analysis and the pixel-level standard deviation across the ten cross-validated models indicated that the predictions for 2000 and 2015 were largely free of extrapolation (less than 0.3% of the pixels; *Supplementary Information* Fig. S10–S11) and showed no spatially clustered uncertainty across the pantropical zone (*Supplementary Information* Fig. S12).

Spatial patterns of HP

In 2015, HP showed important spatial heterogeneity across the tropics (mean HP = 0.70 ± 0.16 ; Fig. 3). The pantropical zone was dominated by high hunting probability with 88% of grid cells exceeded HP > 0.5 and 29% qualified as hotspots (HP > 0.8), whereas only 4% fell in the low-probability range ($0.2 < \text{HP} < 0.4$) and < 0.03% qualified as refuges (HP < 0.2). The realms exhibited different characteristics. The Indomalayan realm was dominated by areas of high HP (48% of cells with a biodiversity index > 0.8; 1% of areas with low HP), the Afrotropics fell at an intermediate level (30% of areas with high HP, 2% of areas with low HP), and the Neotropics showed comparatively lower values (18% of

areas with high HP, 7% of areas with low HP); refuge areas covered less than 0.1% of the 1 × 1 km spatial units.

The largest hotspots, in terms of land area, were in the Indomalayan realm, China, Sri Lanka, the Western Ghats, Peninsular Malaysia, Sumatra, and Java, with additional hotspots in West Africa (Afrotropical) and in the Atlantic Forest, Caribbean islands, southern Mexico, and Guatemala (Neotropical). Refuges clustered in interior Borneo and Papua New Guinea, Central Africa, and the western Amazon Basin. Realm means followed the same gradient: Indomalayan (0.77 ± 0.15) > Afrotropical (0.71 ± 0.13) > Neotropical (0.65 ± 0.13 ; all pairwise $p < 0.001$ Bonferroni; Fig. 3). Low-HP cells were most widespread in the Neotropics (~17%) and rarest in the Indomalayan realm (~6%).

At the country level, HP ranged most widely in the Neotropics (0.50–0.88), then the Afrotropics (0.51–0.83) and Indomalayan realm (0.60–0.88; Fig. 3, *Supplementary Information* Fig. S13). National means were the highest in Sri Lanka and Jamaica (both 0.88 ± 0.09), China (0.85 ± 0.13) and Thailand (0.84 ± 0.11), and were lowest in Guyana (0.50 ± 0.12), Namibia (0.51 ± 0.06) and Somalia (0.54 ± 0.06), the latter two having very small tropical-forest extents.

At the ecoregion level, the Neotropics again showed the widest range (0.47–0.93), followed by Indomalaya (0.50–0.93) and the Afrotropics (0.52–0.86; *Supplementary Information* Fig. S14). High-HP ecoregions included the Northwestern Ghats montane and Malabar Coast moist forests, the Puerto Rican dry and moist forests, and the Chao Phraya freshwater swamp forests. Low-HP ecoregions were remote areas like the

Solimões-Japurá, Juruá-Purus and Uatumã-Trombetas moist forests (Amazon), the Northern New Guinea montane rainforests, and the Northern Triangle temperate forests (northern Myanmar).

Temporal changes in HP

Between 2000 and 2015, HP increased significantly across the tropics (mean change = 0.031 ± 0.083 , $p < 0.001$; hereafter all temporal changes are the absolute difference $HP_{2015} - HP_{2000}$). Most cells changed only modestly (minimum = -0.46 ; 20th percentile = -0.031 ; 40th = 0.0035 ; 60th = 0.040 ; 80th = 0.093 ; maximum = 0.63 ; Fig. 4 & 5). At the realm level, increases were largest in the Indomalayan realm (0.046 ± 0.085) and the Neotropics (0.045 ± 0.087), while the Afrotropics showed a small but significant decline (-0.0054 ± 0.058).

Spatio-temporal patterns differed among realms. In the Indomalayan realm, areas with high HP in 2015 had experienced the largest increases since 2000, while low-HP areas tended to decline, a positive relationship consistent across grid-cell, country and ecoregion scales. The Neotropics and Afrotropics showed no such correlation between 2015 HP and temporal change (Fig. 4; *Supplementary Information Fig. S15–S17*).

At the country level, the Indomalayan countries with the highest 2015 HP also increased the most (China, $+0.084 \pm 0.079$; Thailand, $+0.078 \pm 0.059$), whereas only Myanmar (-0.024 ± 0.061), Cambodia (-0.015 ± 0.080), Papua New Guinea (-0.012 ± 0.057) and Malaysia (-0.009 ± 0.062) declined (*Supplementary Fig. S16 & S18*). In the Neotropics,

increases occurred even in initially low-HP countries (Venezuela, $+0.099 \pm 0.086$; Colombia, $+0.084 \pm 0.069$), with declines in Trinidad and Tobago (-0.031 ± 0.056), Cuba (-0.028 ± 0.063) and to a lesser extent Guyana (-0.006 ± 0.070). The Afrotropics remained stable, with sixteen countries showing minor declines, including Namibia (-0.049 ± 0.064) and Somalia (-0.031 ± 0.040).

Ecoregional trends were like national results. Temporal variability was highest in the Indomalayan realm and positively correlated with 2015 HP. Five ecoregions increased by more than 15%, four in the Neotropics (Orinoco wetlands, Orinoco Delta swamp forests, Cordillera Central páramo, Llanos) and one in Indomalayan realm (the Mentawai Islands rainforests), with the latter combining a large positive change with only intermediate HP (0.65 ± 0.15). Only the Irrawaddy freshwater swamp forests (coastal Myanmar) declined by more than 10%. No Neotropical or Afrotropical ecoregion increased by more than 10%, though several declined by over 5%, the Central Andean dry puna and Tapajós–Xingu moist forests (Neotropics) and the Highveld grasslands (Afrotropics) (Supplementary Fig. S17 & S19).

Discussion

A spatio-temporal index of hunting probability

This study presents a global assessment of hunting probability occurrence across tropical forests using a standardized, non-species-specific measure over time called HP. Unlike previous approaches focused on species-level defaunation and extinction risk^{29,30}, or on IUCN Red List threat assessments as spatial proxies for extinction probability³¹,

our method directly estimates where hunting is likely to occur based on ecological and socio-economic drivers (see also ⁵). Our approach unifies hunting occurrence across motivations (e.g., subsistence and commercial), providing high-resolution global predictions based on observed hunted and non-hunted sites. In contrast to earlier efforts limited to specific realms ⁵ or regional studies ^{26,43} this method provides a cohesive global perspective.

Our HP maps offer a major advance over previous methods not based on specific hunting data that rely on species' threat statuses ³¹ or general infrastructure proximity ²⁰. These maps provide a single, intuitive metric of hunting exposure, making them easily integrable into cumulative threat assessments. This is especially valuable for identifying conservation priority areas, particularly for mammals and birds, which remain disproportionately affected by hunting ^{10,13}. Furthermore, because our index is temporally explicit, it supports the growing need to integrate time-varying threats into conservation planning ⁴².

Ecological and socio-economic drivers of hunting probability

Across all models, accessibility emerged as the strongest and most consistent predictor of HP, confirming prior findings ^{29,30,41}. This relationship was observed globally and within each tropical realm independently (*Supplementary Information, Fig. S15-21*). In all cases, HP increased with proximity to human settlements, with increases beginning at ~25 km and peaking closest to settlements. Forest characteristics also played important roles: large, less-disturbed forest patches adjacent to protected area boundaries showed higher predicted HP, reinforcing the idea that protected areas function as wildlife

reservoirs and their surroundings are prolific hunting grounds^{41,44}. This aligns with recent evidence that species survival often drops rapidly just outside protected areas⁴⁴.

Human population density is typically associated with a broad range of anthropogenic pressures and has been linked to species richness patterns⁴⁵. It is also indirectly included in several global human pressure layers, such as the Forest Landscape Integrity Index²⁰. However, in our analysis, population density did not emerge as an important predictor of hunting exposure. While it is partially correlated with distance to the nearest human settlement, remote sites tend to be in less populated areas, and many sites close to settlements still exhibit very low population density (Supplementary Information, Fig. S20-21). This suggests that hunting likelihood is not confined to densely populated areas. In fact, our results highlight that distance to settlements is a far stronger predictor, indicating that hunting often occurs in less populated but still accessible forested regions, where biodiversity impacts may be more pronounced. Other socio-economic variables, such as GDP and livestock biomass availability, showed effects consistent with theoretical expectations but contributed less to model performance. Collectively, these results underscore the subsistence nature of hunting, which tends to be concentrated in accessible forested landscapes that are not fully disturbed by human infrastructures but not completely remote either.

Spatial patterns

Our predicted spatial patterns of HP partially resemble what has been observed in previous studies^{5,26–30}. Clear hotspots emerged in the Indomalayan realm, especially in China, Sri Lanka, Western India, Peninsular Malaysia, Sumatra, and Java, consistent with

documented patterns of hunting-induced defaunation ^{29,46}. China has been historically recognized as an important destination for illegal wildlife trade, yet recent evidence points out that illegal hunting is also widespread across the country, concentrating towards the east ⁴⁷. In turn, wildlife in Sri Lanka has been subjected to hunting from ca. 45,000 years ago ⁴⁸, and our results indicate that this threat is now pervasive across the island as evidenced by the research devoted to the Indian pangolin (*Manis crassicaudata*) in Sri Lanka ^{49–51}. Additional hotspots were identified in West Africa, across the Atlantic Forest and the Caribbean islands. In contrast, areas of low probability (putative wildlife refuges) were concentrated in remote zones such as interior Borneo, Papua New Guinea, parts of Central Africa, and the western Amazon, reinforcing the role of remoteness and low accessibility in mitigating hunting exposure ^{4,27,28,52}.

Temporal trends

Our results indicate a small but significant global increase in HP from 2000 to 2015. Though the global average was low (~3%), spatial heterogeneity was substantial, with some regions experiencing large increases and others showing declines. Accessibility remained the dominant driver: areas where access expanded, especially near growing village networks, tended to show increased HP. This pattern overlaps with regions of low forest integrity, such as Java, Sumatra, or southeastern China ²⁰, where anthropogenic impacts like fragmentation are already high, and where synergistic effects of both threats could be detrimental for terrestrial wildlife ^{53–55}. Moreover, regions dominated by 'village' anthromes ⁵⁶ largely overlap with areas experiencing increasing HP in our mapping, while 'wildland' anthromes are mostly located in refuge zones. These patterns highlight the importance of understanding how accessibility evolves over time and particularly the

global encroachment of the last remote areas of the planet that hold undisturbed animal communities and maintain ecological integrity ⁵⁷.

Applying hunting exposure in threat mapping

The first target of the Kunming-Montreal Global Biodiversity Framework (KMGBF) emphasizes the need for accurate global mapping of multiple threats to biodiversity. Existing approaches to mapping multiple threats, such as the STAR score ⁵⁸, rely on IUCN threat assessments and are constrained by limited standardization in assessment processes ^{38–40}, taxonomic and geographic biases in assessment robustness ^{37,39,40}, inconsistent application of criteria ^{37–40}, and coarse spatial resolution. Together, these limitations reduce their reliability and restrict their effective integration into decision-making. In contrast, spatially explicit indices such as the Forest Landscape Integrity Index ²⁰ provide useful assessments of landscape-level human disturbance but fail to capture hunting specifically. Unlike our approach, they are not data-driven: hunting is not modelled as a process per se but inferred indirectly from existing human-presence proxies. The HP maps developed in this study help fill this gap. They offer a standardized, species-independent, and continuous measure of hunting probability, ranging from 0 to 1, at fine spatial resolution (1 km²). This makes them directly compatible with other global threat layers and highly suitable for integration into cumulative threat mapping, thereby contributing to KMGBF Target 1 by supporting spatial prioritization of conservation action in response to multiple threats. Specifically, it can be combined with other spatial threat layers like the Forest Landscape Integrity Index ²⁰, the Human Modification Index ^{33,59} or the Human Footprint ^{19,60} to create composite indices. Importantly, by excluding biodiversity data from the HP metric itself, we preserve its flexibility for diverse

applications. Hunting can affect biodiversity through multiple pathways like reducing population densities, altering species behavior or reshaping community composition through selective harvest of particular taxonomic groups, all of which can cascade into broader changes in functional and phylogenetic diversity. By keeping the HP layer independent, researchers and practitioners can combine it with the biodiversity datasets most relevant to their objectives, whether to disentangle the specific contribution of hunting exposure to observed patterns in species richness or abundance (e.g.,⁶¹), or to assess its downstream effects on taxonomic, functional, and phylogenetic diversity across taxa (e.g.,¹⁴). This versatility is further supported by the high resolution and predictive performance of our modeling approach. Consequently, future efforts should aim to couple spatially explicit hunting models with biodiversity data to prioritize conservation actions more effectively. A key application could be the integration of HP into spatially explicit vulnerability frameworks, such as that developed by Boyce et al.⁶², which disaggregate vulnerability into exposure, sensitivity, and adaptive capacity. In such approaches, HP can serve as an exposure layer, analogous to how climatic variables are used in climate vulnerability assessments, to quantify the spatial distribution of hunting risk and provide a robust, transferable foundation for assessing exposure to hunting and improving spatial decision-making for conservation under the KMGBF.

However, although our HP layer is provided at 1 km² resolution, chosen for compatibility with other global threat layers, the effective interpretable resolution is coarser, bounded by (i) the typical spatial footprint of the primary studies providing training data, (ii) the native resolution of predictors such as HDI, GDP or domestic meat biomass (high-resolution data obtained from downscaling) and (iii) the existing (but limited) spatial autocorrelation structure of the residuals (see SAC analyses in Methods). We recommend

interpreting HP at scales of ~10–50 km for regional comparisons or larger aggregations (country, ecoregion, realm) for policy-oriented analysis, and caution against treating individual 1 km pixels as site-level predictions for local conservation planning, for which direct field assessment remains essential.

Limitations and future directions

The HP metric developed here is a probability of hunting occurrence rather than a measure of hunting intensity, magnitude or ecological impact. Two sites with equal HP may in practice experience very different hunting rates (occasional vs systematic), and this simplification is unavoidable given the binary nature of the training data. The 'non-hunted' class is defined as 'sites for which no hunting activity is reported in the primary literature' and is therefore a best-available approximation of a true absence: absence of a report is not the same as absence of the activity. We therefore urge users to treat HP as a spatially explicit exposure layer rather than as a direct measure of hunting-induced biodiversity loss, for which alternative approaches exist ^{29,30}.

Another methodological direction that could be explored to further refine the hunting exposure layers is to disaggregate the exposure exerted by hunting according to its purpose. Subsistence or commercial hunting (pet or product trade), differ in their magnitude of impact ⁴, spatial patterns (¹⁴ for pet vs product trade), targeted species (e.g., ¹² for traded passerines), and management needs. Developing separate models for these distinct hunting types would allow for more targeted conservation planning. For example, pangolins are the most trafficked species in the world, with all eight species being threatened to different levels due to the international demand of their scales by traditional

medicine and the use of their meat as a luxury product^{65,66}, yet meat consumption by local populations can also exert significant impacts on their populations⁶⁷.

While global threat mapping studies have become increasingly common⁶⁸, some authors criticize that these approaches are overly technocratic and insufficiently connected to local knowledge, practices, and cultural contexts⁶⁹. These concerns are particularly important for hunting, a highly context-dependent activity shaped by local biodiversity, cultural beliefs and taboos, and socio-economic conditions^{41,70,71}. Accordingly, and as discussed throughout this study, our HP maps are not intended to be used in isolation to prioritize conservation actions. Rather, they provide a robust, high-resolution, and standardized layer of potential hunting exposure, designed to be integrated with independent biodiversity information, including species distributions, abundance, richness, sensitivity, and the presence of indigenous communities, to identify areas where hunting exposure and conservation priorities overlap, thereby guiding evidence-based spatial prioritization. Crucially, we assign no normative value to hunting itself. Hunting can be detrimental to biodiversity and human well-being when unsustainable, yet when well-managed it represents an integral component of many cultures, local economies, and socio-ecological systems⁷².

Methods

Data collection

We retrieved spatial information of the occurrence of non-hunted and hunted forest sites (coded as 0 and 1, respectively). To this end, we relied on extended versions of the most comprehensive dataset of hunting impacts on bird and mammal populations of Benítez-López et al.²⁴ which incorporated additional sites from local hunting studies^{29,30}. The

original dataset comprises data on abundance of tropical birds and mammal species across pairwise hunted and non-hunted forest sites from 176 studies. Non-hunted sites were defined as areas with no evidence of hunting activity, as assessed by the authors of the hunting studies. Examples include areas where snare densities were zero and located at least >40 km from the nearest village, or sites entirely uninhabited by forest dwellers, with no evidence of hunting activity (e.g. shotguns, hunting trails, old campsites...), and not accessible to hunters due to geographic isolation or strict protection. This dataset was recently updated by carrying out the same systematic literature review for studies published between 2017 and 2022 in Web of Science and Google Scholar using the same search string: "road* OR settlement* OR village OR infrastructure* + access* OR intersection OR distance OR disturbance OR proximity AND hunting* OR bushmeat OR poaching OR trade AND diversity OR population OR abundance* OR *density OR encounter". Relevant grey literature (i.e., reports or PhD and MSc thesis) as studies in Spanish and Portuguese were further identified by cross-reference. Studies included in the database report abundances at hunted and non-hunted sites without any potential confounding effect (e.g., logging, gold mining). For each study included in this database, we extracted latitude and longitude of each hunted and non-hunted sites when reported, or georeferenced them using GIS if the coordinates were not available. When the hunted and non-hunted sites in this database were aggregated according to ecological and landscape similarities, we consulted the original studies and extracted the coordinates of all points reported as hunted or non-hunted, thereby increasing the number of locations of hunting occurrence compared to the total originally reported in the databases. Additionally, we performed targeted searches for countries not represented in the dataset using Web of Science (detailed in *Supplementary Information*), from which we extracted, when available, relevant spatial information on

hunting activities, and were thus included in our dataset. Through this process, we obtained 2,463 hunted and non-hunted sites spread across the three tropical realms, Afrotropical, Indomalayan and Neotropical (*Supplementary Information*, Fig. S24). We observed an imbalance in sites, firstly in terms of hunted ($n_{\text{Xh}} = 1,762$) vs. non-hunted ($n_{\text{Xc}} = 701$) sites, and secondly in terms of spatial distribution across biogeographical realms: 331 in the Afrotropics, 412 in the Indomalayan realm, and 1,720 in the Neotropics (see below).

We selected several socio-economic and ecological predictors known to influence hunting practices in tropical forests^{5,29,30}. Accessibility-related predictors included distance to the nearest human settlement (km), distance to the nearest water body (km)⁷³, and distance to protected area boundaries (km; IUCN categories I–IV,⁷⁴), all calculated at a 1 × 1 km grid-cell resolution. Urban market accessibility was also calculated at 1 × 1 km resolution and expressed as travel time to the nearest town or city with ≥ 50,000 inhabitants (minutes)^{75,76}. Availability of domestic meat as an alternative protein source (kg/km²) was computed at 1 × 1 km resolution for the years 2010, 2015, and 2020⁷⁷, and subsequently aggregated (here and after using the average) to 20 × 20 km grid cells. Socio-economic predictors included gridded revised real gross domestic product (GDP; million USD)⁷⁸ and the Human development index (HDI; unitless score ranging from 0 [lowest development] to 1 [highest development])⁷⁹, both derived from national and subnational data. These variables were calculated at 1 × 1 km resolution and aggregated to 20 × 20 km grid cells. Human population density (individuals/km²) for the years 2000–2020⁸⁰ was also aggregated to 20 × 20 km resolution. Ecological predictors comprised forest cover (%)⁸¹ calculated within 1 km and 20 km radius buffers, net primary productivity (gC/m²/year)⁸², and mean slope (degrees)⁸³, all measured at 1 km² resolution

(see Table 1 for the rationale behind predictor selection). All predictors were masked for the pantropical forest zone, which includes areas with at least 20% forest cover¹⁶. Except for distance to the nearest human settlement, we extracted predictor values for each study site directly from raster layers at the highest available spatial resolution, matching them as closely as possible to the year of data collection reported in the study. Of the 12 predictors used, 10 are time-varying (distance to the nearest human settlement, distance to protected areas, population density, GDP, HDI, travel time to cities, forest cover, and domestic meat biomass availability & NPP) and 2 are static within the 2000–2015 window (distance to water bodies). Additionally, when an exact temporal match was not available, we used either the closest available year or interpolated the value by averaging the two nearest temporal layers. Distance to the nearest water body and mean slope were treated as static variables and therefore do not require temporal matching with hunting observations. Mean slope was derived from terrain topography⁸³, while water bodies were defined using current permanent water bodies reconstructed from satellite time series spanning 1984–2021⁷³. We deliberately restricted this variable to permanent water bodies to ensure that it reflects generally accessible water sources rather than short-term or seasonal events. This approach avoids introducing temporal variability in water availability that would not correspond to how hunting presence was measured, which was not directly linked to a specific point in time. The distances to the nearest settlement were extracted manually from each study using information provided by the authors (e.g., direct measure, maps) or by georeferencing hunted and non-hunted sites over satellite images. The collected data are provided with the manuscript, except for certain sites subject to confidentiality agreements due to illegal hunting, all extracted from a single study conducted in Madagascar (see *Data availability statement*). Urban market accessibility, measured as travel time to the nearest city with $\geq 50,000$ inhabitants, was

derived from two datasets (for the years 2000 and 2015), each developed using different methodologies. This mismatch could introduce biases. To evaluate this, we conducted additional analyses presented in the *Supplementary Information* Fig. S20–S21, S23–S24. These include comparisons of values across time layers and assessments of their influence on model predictions. Although not perfect, these steps help account for potential temporal inconsistencies and methodological differences, reducing the risk of systematic bias in our modeling. Additionally, data on the availability of domestic meat as an alternative food source were only available for 2010, 2015, and 2020, which may reduce the accuracy of this predictor for older hunting records and for the 2000 hunting probability map. We acknowledge this limitation and conducted exploratory analyses presented in the *Supplementary Information* to assess the potential bias introduced by this temporal mismatch (*Supplementary Information* Fig. S20-25).

Model building

After compiling the dataset containing site-level information, hunting status (i.e., hunted = 1; non-hunted = 0), and associated ecological and socio-economic predictors, we built supervised learning models to classify the hunting status of each site. We chose random forests for this task — a tree-based algorithm well suited for handling non-linear relationships and complex interactions among predictors, which we expected *a priori*. To address both spatial heterogeneity and the imbalance between hunted and non-hunted sites, we implemented six different training-validation and testing strategies. Because we lacked a true out-of-sample dataset for independent validation, we used two cross-validation splitting schemes: random splitting (80% training-validation, 20% testing) and spatial blocking (block size = 5), using the *cv_spatial()* function from the *blockCV* R package⁸⁴. To deal with class imbalance within the training-validation

491 datasets, we applied three approaches: SMOTE (Synthetic Minority Oversampling
492 Technique), implemented via *smote()* in the *smotefamily* R package⁸⁵, class weighting to
493 increase the importance of under-represented non-hunted sites and downsampling of
494 the majority (hunted) class. Additionally, each model was fine-tuned using Monte Carlo
495 cross-validation (MCCV), which is appropriate for binary classification with small sample
496 sizes⁸⁶ (detailed in *Supplementary Information* Fig. S2-S5 & S26).

497
498 To further limit overfitting and increase robustness, we repeated this entire process 10
499 times using 10 different training-validation testing splits for each strategy. This generated
500 ten final models per strategy. Using multiple models, rather than a single final one,
501 allowed us to account for variability in model outcomes due to regional heterogeneity in
502 hunting patterns, ensuring more generalizable predictions across the full tropical domain.

504 *Model performance*

505 We evaluated the goodness-of-fit of the fine-tuned models by comparing the observed
506 and predicted hunting status in the testing datasets. For this, we used the *predict()*
507 function of the *randomForest* R package⁸⁷ and assessed random forests performance
508 using 5 standard metrics: Matthew correlation coefficient (MCC), F1-score, area under
509 the Receiver Operating Curve (AUC), true positive rate (TPR) and true negative rate (TNR).
510 These metrics were computed for each of the 10 training-validation testing splits across
511 all six modelling strategies. We also assessed whether calibration of model predictions
512 was necessary, following recommendations by Dormann⁸⁸ (detailed in *Supplementary*
513 *Information* Fig. S6).

515 Additionally, we investigated the relationships between dependent and independent
516 predictors using two primary methods. First, we calculated the mean absolute SHAP
517 (Shapley Additive exPlanations) values to assess the importance of each predictor. This
518 calculation was conducted using the `sv_importance()` function from the `shapviz` R
519 package⁸⁹. We examined the marginal effects of each predictor by plotting the covariate
520 against its corresponding SHAP value for each observation from the fine-tuned models.
521 This method allows for a clear interpretation of how each feature influences the model's
522 predictions. Independent predictors were transformed when necessary but only for visual
523 purposes.

524
525 We assessed residual spatial autocorrelation (SAC) in the random forests using global
526 Moran's I computed on out-of-bag residuals across four distance classes (0, 250, 1000
527 and 2500 km). Additionally, we compared the non-spatial model with a spatial random
528 forest augmented with Moran's eigenvector maps under spatially blocked cross-
529 validation (`blockCV`, 500 km blocks). Residual SAC was low at every distance class
530 (Moran's I = 0.017–0.030; all $p < 0.001$ given $n = 2,463$; *Supplementary Information* Fig.
531 S9), well below conventional effect-size thresholds for RF-based ecological predictions.
532 The MEM-augmented spatial RF yielded comparable Moran's I (0.018–0.037) and near-
533 identical `blockCV` performance (AUC 0.80 ± 0.10 vs 0.80 ± 0.11). Because MEM
534 correction did not reduce SAC further nor change predictive performance, we retained
535 the non-spatial random forest for model predictions.

536 537 *Predictions*

538 The strategy selected to predict hunting probability (HP) across the entire pantropical
539 forest zone at a 1 km × 1 km resolution was calibrated non-spatial random forests trained

with random splitting and combined with downsampling, which achieved the best performance across the five goodness-of-fit metrics (see *Supplementary results - Model performance* Fig. S2). As each modeling strategy was evaluated using multiple training-validation vs. testing splits, resulting in one fine-tuned random forest per split, we adopted an ensemble prediction strategy. For each grid cell, we computed the median hunting probability across all models from the best-performing approach to produce a robust, spatially explicit estimate of HP. The predictor values used for generating predictions were consistent with those previously described (section *Data Collection*), except for the distance to the nearest settlement. For this predictor, we used the World Settlement Footprint dataset⁹⁰ filtered to remove urban areas to create distance-to-settlement layers for both 2000 and 2015, as detailed in the *Supplementary Information*.

To assess temporal changes in HP, we compared model outputs between the years 2000 and 2015. This time window was chosen due to the availability of consistent and comprehensive data layers (Table 1). We quantified both the 2015 HP and the absolute difference between 2015 and 2000 values (hereafter referred to as 'change'). We classified hunting probability into three categories based on model uncertainty: hotspots ($HP > 0.8$), low-probability areas ($0.2 < HP < 0.4$), and potential refugia ($HP < 0.2$). Values above 0.8 and below 0.2 correspond to high-confidence predictions, where the probability of misclassification is low. In contrast, predicted probabilities around 0.5 represent the highest uncertainty, as 0.5 was the threshold used to convert probabilities into binary outputs (0 = no hunting; 1 = hunting) during model evaluation. Because uncertainty is maximal near this decision threshold, we defined the “low-probability” category using the range 0.2–0.4 to capture areas predicted as hunted with moderate

confidence but below the binary classification threshold, while avoiding the zone of highest uncertainty around 0.5.

Extrapolation of predictions beyond the environmental envelope of the training data was assessed with a Multivariate Environmental Similarity Surface (MESS) and pixel-level predictive uncertainty was quantified as the standard deviation of predicted hunting probability across the ten cross-validated random-forest models (*Supplementary Information Fig. S10 & S11*).

We assessed the statistical significance of changes and realm-level differences using Student's t-tests, implemented with the *t.test()* function in R. Both one-sample and two-sample t-tests were used, applying Bonferroni corrections for multiple comparisons. In addition, we investigated finer-scale spatial variation by aggregating values for both 2015 HP and the change in HP to calculate means and standard deviations at the country and ecoregion levels, based on national borders and coastlines from the public-domain "Natural Earth" dataset accessed via the *rnaturalearth* R package⁹¹ and the ecoregions defined by Olson et al.⁹².

Maps

All maps were created using national borders and coastlines and are sourced from the public-domain "Natural Earth" dataset using the R package *rnaturalearth*⁹¹.

Data availability statement

All data and models produced in this study are available in a single Zenodo repository (<https://doi.org/10.5281/zenodo.20699529>), organized as an R project

('Hunting_probability_R_proj') that can be run directly by following the instructions in the associated README files. The repository also includes raster layers of the mean and standard deviation of hunting probability and Supplementary Tables 1–3. A subset of occurrence records subject to confidentiality agreements has been withheld to protect the identities of communities engaged in the illegal activities described in ref. ⁹³ and cannot be made public. Access to this restricted subset is controlled to protect the safety and identities of communities engaged in activities described as illegal in the source study, in accordance with the data use agreement under which it was obtained. Requests for access may be directed to the corresponding author of the reference cited above

Code availability

All R scripts used to train and fine-tune the random forest models presented in this study are available in the same Zenodo repository as the data (<https://doi.org/10.5281/zenodo.20699529>), organized as the R project 'Hunting_probability_R_proj'.

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Author contributions

A.B.-L. conceived the original idea. M.P.-L. and A.B.-L. designed the research. M.P.-L., I.F.-A., L.M.-P., and A.B.-L. performed the initial research. D.S. and J.F.B. provided additional data. M.P.-L. led the modeling, with contributions from L.M.-P., and analyzed the model outputs. I.F.-A. and A.B.-L. advised on framework conception, modeling, and interpretation of results. I.F.-A., D.S., J.F.B., L.M.-P., and A.B.-L. contributed to writing and reviewing the manuscript. M.P.-L. led the writing.

Competing interests

The authors declare no competing interests.

629 **Table 1. Predictors used in the models, with data sources, temporal and spatial resolution, and its expected relationship**
630 **with hunting likelihood occurrence**

Predictor	Expected relationships	Source	Spatial resolution	Collecting years
Distance to the nearest human settlement	According to the central place foraging hypothesis, decaying hunting probability is usually related to the distance to small towns and villages. Hence, we expect that hunting probability would decrease with distance to human settlements.	⁹⁰	30 m x 30 m	2000, 2015
Distance to the nearest water body		⁷³ Source: EC JRC/Google	30 m x 30 m	1984 - 2021
Minimum distance to protected area (PA) boundaries	PAs may attract hunters due to higher wildlife abundance but also benefit from enforcement. We therefore expected hunting probability to peak at PA edges and decline beyond.	⁷⁴	Polygons	2000 - 2024
Accessibility to urban markets	Travel time to major towns is commonly used as a proxy for accessibility to urban markets, where wildlife products such as bushmeat, animal parts, or live animals can be sold. Shorter travel times reduce the costs and effort required to transport hunted	^{75,76}	1 km x 1 km	2000, 2015

	goods, thereby increasing the incentive for hunters to operate in those areas. As a result, areas closer to major towns are generally associated with higher hunting probability driven by commercial trade.			
Availability to domestic meat	Greater availability of domestic meat is expected to reduce reliance on wild meat for subsistence, as it provides an accessible and reliable alternative protein source. This shift in dietary dependence may lead communities to hunt less, particularly in areas where hunting is primarily driven by the need for food rather than commercial trade, thereby reducing overall hunting occurrence.	85	1 km x 1 km 20 km x 20 km	2010, 2015, 2020
Gridded revised real gross domestic product based on national and subnational data	The relationship between hunting and wealth is complex and context-dependent, often varying between rural and urban settings ⁷⁸ . In rural areas, wildlife meat consumption tends to decline with increasing wealth, while in urban areas, it may increase due to demand for exotic or luxury products. Additionally, wildlife trade can serve as a significant income source for rural communities, especially in remote areas where rare species can fetch high market prices. Considering these factors, we expected higher hunting probability in poorer regions due to subsistence needs, but also some positive association with wealthier areas where wildlife products are valued as luxury commodities.	78	1 km x 1 km 20 km x 20 km	2000 - 2020
Gridded revised Human development index based on national and		79	1 km x 1 km 20 km x 20 km	1990 - 2015

subnational data				
Human population density		80	1kmx1km	2000, 2005, 2010, 2015, 2020
Forest cover	Hunting probability is typically higher in healthier, less-degraded forests, where wildlife is more abundant and easier to encounter. These areas also tend to support rarer, specialist species that can be specifically targeted due to their high market value, further increasing hunting activity.	81	30 m x 30 m	2000, 2005, 2010, 2015, 2020
Net primary productivity		82	1 km x 1 km	2001 - 2021
Elevation and ground slope	Hunting probability is generally lower in steep, less accessible areas due to the physical difficulty of reaching these sites, making hunting less efficient and less rewarding.	83	1 km x 1 km	2024

632 **Figure Legends/Captions**

633

634 **Figure 1. Spatial distribution of hunted and non-hunted sites extracted from the primary literature (n = 2,463) across the**
635 **pantropical forest zone.** Points are coloured by biogeographic realm (green: Neotropical; orange: Afrotropical; blue: Indomalayan);
636 darker circles indicate hunted sites and crosses non-hunted sites. The stacked bar chart (right) summarizes the number of hunted
637 (darker shades) and non-hunted sites (paler shades) per realm. The pale green background shows the pantropical forest zone
638 analyzed in this study.

Figure 2. Key ecological and socioeconomic variables predicting hunting probability occurrence.

In panel A, the overall importance of each predictor, quantified as the mean absolute SHAP (SHapley Additive exPlanations) value and averaged across ten cross-validated models, is shown by the bar height; black error bars indicate ± 1 SD across the ten models, and open circles show the ten individual per-model mean absolute SHAP values. The color gradient defines the mean absolute SHAP value, with lighter colors (yellow) indicating higher importance and darker colors (black to purple) indicating lower importance. In panel B, SHAP dependence plots showing the effects of the six most globally important predictors (based on mean absolute SHAP values) on the predicted probability that a site is classified as hunted. Each point represents an individual site prediction derived from ecological and socio-economic variables using trained random forest classifiers. Positive SHAP values indicate an increased likelihood of a site being classified as hunted, whereas negative values indicate an association with non-hunted status. Non-linear regression lines illustrate the shape of each predictor's effect, fitted using generalized additive models (GAM), and the shaded band around each line represents the 95% confidence interval of the GAM smooth. Mean absolute SHAP values are additionally shown to summarize overall predictor importance across models. Distance to settlements is expressed in kilometres (km), forest cover as a proportion in a 20 km buffer, the Human development index as a unitless score, livestock biomass as the square-root-transformed kg km^{-2} , and net primary productivity in $\text{g C m}^{-2} \text{ yr}^{-1}$.

Figure 3. Spatial variation in predicted Hunting Probability across tropical forests in 2015. Hunting Probability corresponds to probability of a site of being exposed to hunting occurrence and was predicted for each 1 km × 1 km grid cell using spatially explicit environmental and socio-economic predictors from ca. 2015. Predictions represent the median values from 10 independently trained and fine-tuned random forest models, each calibrated using random cross-validation and downsampling to address class imbalance (hunted vs. non-hunted sites). Hunting probability is displayed on a continuous scale from 0 to 1, with color breaks at 0.1 intervals. Insets A, B, and C provide zoomed views of heterogeneous areas where low and high hunting probability occur within the Neotropics, Afrotropics, and Indomalayan realms, respectively. The bottom-right inset displays the same map, highlighting grid cells with hunting probability > 0.8 (red; hotspots), 0.2–0.4 (cyan; low-probability areas), and < 0.2 (blue; potential refuges). The colour bar associated with each realm indicates the percentage of cells falling within each of these three classes.

Figure 4. Spatio-temporal variation in predicted Hunting Probability across tropical forests between 2000 and 2015, by biogeographic realm. Each box shows the density distribution of predicted Hunting Probability in 2015 and the change in probability between 2000 and 2015 across 1 km × 1 km grid cells within each biogeographic realm. Change is calculated as the difference between predicted probability in 2015 and 2000, where negative values indicate a decrease and positive values an increase in exposure. Color intensity represents the relative probability density, ranging from darker shades (values around the median, with ~50% of cells) to lighter shades (covering up to 99% of the observed values).

Figure 5. Spatio-temporal variation in predicted Hunting Probability across tropical

forests between 2000 and 2015. Hunting Probability corresponds to probability of a site

of being hunted and was predicted at a 1 km × 1 km resolution using spatially explicit

environmental and socio-economic predictors from 2000 and 2015 (or the closest

available years). Predictions correspond to the median values from 10 independently

trained and fine-tuned random forest models, calibrated using random cross-validation

and downsampling to correct for class imbalance (hunted vs. non-hunted sites). The

Hunting Probability values represent predictions for 2015, while change values indicate

the difference between 2015 and 2000 predictions, where negative values reflect a

decrease and positive values an increase in exposure over time. Both metrics are

categorized by percentiles (0–20%, 20–40%, 40–60%, 60–80%, 80–100%).

Combinations of probability and temporal change quantiles are color-coded as grey: low

probability and decreasing probability, yellow: high probability and decreasing

probability, blue: low probability and increasing probability or purple: high probability and

increasing probability. Insets A, B, and C provide zoomed views of heterogeneous areas

where different hunting probability patterns occur within the Neotropics, Afrotropics, and

Indomalayan realms, respectively.

References

1. Malhi, Y. et al. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl Acad. Sci.* **113**, 838–846 (2016).
2. Douglass, K. et al. Late Pleistocene/Early Holocene sites in the montane forests of New Guinea yield early record of cassowary hunting and egg harvesting. *Proc. Natl Acad. Sci.* **118**, e2100117118 (2021).
3. Ripple, W. J. et al. Bushmeat hunting and extinction risk to the world's mammals. *R. Soc. Open Sci.* **3**, 160498 (2016).
4. Benítez-López, A. et al. The impact of hunting on tropical mammal and bird populations. *Science* **356**, 180–183 (2017).
5. Bogoni, J. A., Peres, C. A. & Ferraz, K. M. P. M. B. Extent, intensity and drivers of mammal defaunation: a continental-scale analysis across the Neotropics. *Sci. Rep.* **10**, 14750 (2020).
6. Stafford, C. A., Preziosi, R. F. & Sellers, W. I. A Cross-Site Analysis of Neotropical Bird Hunting Profiles. *Trop. Conserv. Sci.* **10**, 1940082917736894 (2017).
7. Santos-Fita, D., Naranjo, E. J. & Rangel-Salazar, J. L. Wildlife uses and hunting patterns in rural communities of the Yucatan Peninsula, Mexico. *J. Ethnobiol. Ethnomedicine* **8**, 38 (2012).
8. Scheffers, B. R., Oliveira, B. F., Lamb, I. & Edwards, D. P. Global wildlife trade across the tree of life. *Science* **366**, 71–76 (2019).
9. Morton, O., Scheffers, B. R., Haugaasen, T. & Edwards, D. P. Impacts of wildlife trade on terrestrial biodiversity. *Nat. Ecol. Evol.* **5**, 540–548 (2021).

- 723 10. Challender, D. W. S. et al. Identifying species likely threatened by international trade
724 on the IUCN Red List can inform CITES trade measures. *Nat. Ecol. Evol.* **7**, 1211–
725 1220 (2023).
- 726 11. Brodie, J. F. et al. Defaunation impacts on the carbon balance of tropical forests.
727 *Conserv. Biol.* **39**, e14414 (2025).
- 728 12. Senior, R. A., Oliveira, B. F., Dale, J. & Scheffers, B. R. Wildlife trade targets colorful
729 birds and threatens the aesthetic value of nature. *Curr. Biol.* **32**, 4299–4305.e4
730 (2022).
- 731 13. Hughes, L. J., Morton, O., Scheffers, B. R. & Edwards, D. P. The ecological drivers
732 and consequences of wildlife trade. *Biol. Rev.* **98**, 775–791 (2023).
- 733 14. Hughes, L. J. et al. Global hotspots of traded phylogenetic and functional diversity.
734 *Nature* **620**, 351–357 (2023).
- 735 15. Almeida, R. J., Mazza, A. N. & Lockwood, J. L. Does fortune follow function?
736 Exploring how consumer preferences drive the functional trait composition of the
737 global songbird trade. *People Nat.* **6**, 1366–1377 (2024).
- 738 16. Potapov, P. et al. The last frontiers of wilderness: Tracking loss of intact forest
739 landscapes from 2000 to 2013. *Sci. Adv.* **3**, e1600821 (2017).
- 740 17. Malhi, Y., Gardner, T. A., Goldsmith, G. R., Silman, M. R. & Zelazowski, P. Tropical
741 Forests in the Anthropocene. *Annu. Rev. Environ. Resour.* **39**, 125–159 (2014).
- 742 18. Venter, O. et al. Sixteen years of change in the global terrestrial human footprint and
743 implications for biodiversity conservation. *Nat. Commun.* **7**, 12558 (2016).
- 744 19. Venter, O. et al. Global terrestrial Human Footprint maps for 1993 and 2009. *Sci.*
745 *Data* **3**, 160067 (2016).

- 746 20. Grantham, H. S. et al. Anthropogenic modification of forests means only 40% of
747 remaining forests have high ecosystem integrity. *Nat. Commun.* **11**, 5978 (2020).
- 748 21. Joppa, L. N. et al. Filling in biodiversity threat gaps. *Science* **352**, 416–418 (2016).
- 749 22. Redford, K. H. The Empty Forest: Many large animals are already ecologically
750 extinct in vast areas of neotropical forest where the vegetation still appears intact.
751 *BioScience* **42**, 412–422 (1992).
- 752 23. Wilkie, D. S., Bennett, E. L., Peres, C. A. & Cunningham, A. A. The empty forest
753 revisited. *Ann. N. Y. Acad. Sci.* **1223**, 120–128 (2011).
- 754 24. Dirzo, R. et al. Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
- 755 25. Deith, M. C. M. & Brodie, J. F. Predicting defaunation: accurately mapping
756 bushmeat hunting pressure over large areas. *Proc. R. Soc. B Biol. Sci.* **287**,
757 20192677 (2020).
- 758 26. Ziegler, S. et al. Mapping Bushmeat Hunting Pressure in Central Africa. *Biotropica*
759 **48**, 405–412 (2016).
- 760 27. Antunes, A. P. et al. Wild meat hunting in the Amazon. *Nature* **641**, 134–141 (2025).
- 761 28. Bessone, M. et al. Bushmeat offtake across Central Africa. *Nature* **653**, 1092–1098
762 (2025).
- 763 29. Benítez-López, A., Santini, L., Schipper, A. M., Busana, M. & Huijbregts, M. A. J.
764 Intact but empty forests? Patterns of hunting-induced mammal defaunation in the
765 tropics. *PLOS Biol.* **17**, e3000247 (2019).
- 766 30. Ferreira-Arias, I. et al. Drivers and spatial patterns of avian defaunation in tropical
767 forests. *Divers. Distrib.* **31**, e13855 (2025).
- 768 31. Harfoot, M. B. J. et al. Using the IUCN Red List to map threats to terrestrial
769 vertebrates at global scale. *Nat. Ecol. Evol.* **5**, 1510–1519 (2021).

- 770 32. Ellis, E. C. et al. People have shaped most of terrestrial nature for at least 12,000
771 years. *Proc. Natl. Acad. Sci.* **118**, e2023483118 (2021).
- 772 33. Theobald, D. M. et al. Global extent and change in human modification of terrestrial
773 ecosystems from 1990 to 2022. *Sci. Data* **12**, 606 (2025).
- 774 34. Jacobson, A. P., Riggio, J., M. Tait, A. & E. M. Baillie, J. Global areas of low human
775 impact ('Low Impact Areas') and fragmentation of the natural world. *Sci. Rep.* **9**,
776 14179 (2019).
- 777 35. Riggio, J. et al. Global human influence maps reveal clear opportunities in
778 conserving Earth's remaining intact terrestrial ecosystems. *Glob. Change Biol.* **26**,
779 4344–4356 (2020).
- 780 36. Pacifici, M., Cristiano, A., Mancini, G., Nania, D. & Davoli, M. Global hotspots of
781 bushmeat hunting risk for mammals. Preprint at [https://doi.org/10.21203/rs.3.rs-](https://doi.org/10.21203/rs.3.rs-6278255/v1)
782 [6278255/v1](https://doi.org/10.21203/rs.3.rs-6278255/v1) (2025).
- 783 37. Humphries, E. et al. Evaluating the empirical basis for threat attribution in the IUCN
784 Red List. *Conserv. Biol.* **n/a**, e70213.
- 785 38. Cazalis, V. et al. Bridging the research-implementation gap in IUCN Red List
786 assessments. *Trends Ecol. Evol.* **37**, 359–370 (2022).
- 787 39. Hughes, A., Orr, M. C., Palacio, R. D., Xuan, Y. & Qiao, H. A dire need for better
788 standards of data quality, transparency, and reproducibility in IUCN RedList
789 assessments. <https://ecoevorxiv.org/repository/view/7081/> (2024).
- 790 40. Palacio, R. D. et al. The global influence of the IUCN Red List can hinder species
791 conservation efforts. <https://doi.org/10.22541/au.169945445.50394320/v1> (2023)
792 [doi:10.22541/au.169945445.50394320/v1](https://doi.org/10.22541/au.169945445.50394320/v1).
- 793 41. Ingram, D. J. et al. Regional patterns of wild animal hunting in African tropical
794 forests. *Nat. Sustain.* **8**, 202–214 (2025).

- 795 42. Ma, J., Li, J., Wu, W. & Liu, J. Global forest fragmentation change from 2000 to
796 2020. *Nat. Commun.* **14**, 3752 (2023).
- 797 43. Nguimdo, V. R. V. et al. Long-Term Monitoring of Hunting Signs Reveals Complex
798 Spatiotemporal Patterns of Hunting Activities in an Unprotected African Rainforest.
799 *Divers. Distrib.* **31**, e13951 (2025).
- 800 44. Semper-Pascual, A. et al. Occurrence dynamics of mammals in protected tropical
801 forests respond to human presence and activities. *Nat. Ecol. Evol.* **7**, 1092–1103
802 (2023).
- 803 45. Greco, I. et al. Landscape-level human disturbance results in loss and contraction
804 of mammalian populations in tropical forests. *PLOS Biol.* **23**, e3002976 (2025).
- 805 46. Redmond, I. M. Recipes for Survival: Controlling the Bushmeat Trade. Ape Alliance
806 report funded by WSPA. Ape Alliance Rep.
807 [https://www.academia.edu/43704242/Recipes_for_Survival_Controlling_the_Bushm](https://www.academia.edu/43704242/Recipes_for_Survival_Controlling_the_Bushmeat_Trade_Ape_Alliance_report_funded_by_WSPA)
808 [eat_Trade_Ape_Alliance_report_funded_by_WSPA](https://www.academia.edu/43704242/Recipes_for_Survival_Controlling_the_Bushmeat_Trade_Ape_Alliance_report_funded_by_WSPA) (2006).
- 809 47. Liang, D., Giam, X., Hu, S., Ma, L. & Wilcove, D. S. Assessing the illegal hunting of
810 native wildlife in China. *Nature* **623**, 100–105 (2023).
- 811 48. Wedage, O. et al. Specialized rainforest hunting by *Homo sapiens* ~45,000 years
812 ago. *Nat. Commun.* **10**, 739 (2019).
- 813 49. Perera, P. K. P., Karawita, K. V. D. H. R. & Pabasara, M. G. T. Pangolins (*Manis*
814 *crassicaudata*) in Sri Lanka: A Review of Current Knowledge, Threats and Research
815 Priorities. *J. Trop. For. Environ.* **7**, (2017).
- 816 50. Karawita, H., Perera, P., Gunawardane, P. & Dayawansa, N. Habitat preference and
817 den characterization of Indian Pangolin (*Manis crassicaudata*) in a tropical lowland
818 forested landscape of southwest Sri Lanka. *PLOS ONE* **13**, e0206082 (2018).

- 819 51. Perera, P. & Karawita, H. An update of distribution, habitats and conservation status
820 of the Indian pangolin (*Manis crassicaudata*) in Sri Lanka. *Glob. Ecol. Conserv.* **21**,
821 e00799 (2020).
- 822 52. Brodie, J. F. et al. Landscape-scale benefits of protected areas for tropical
823 biodiversity. *Nature* **620**, 807–812 (2023).
- 824 53. Peres, C. A. Synergistic Effects of Subsistence Hunting and Habitat Fragmentation
825 on Amazonian Forest Vertebrates. *Conserv. Biol.* **15**, 1490–1505 (2001).
- 826 54. Sreekar, R. et al. The use of species–area relationships to partition the effects of
827 hunting and deforestation on bird extirpations in a fragmented landscape. *Divers.*
828 *Distrib.* **21**, 441–450 (2015).
- 829 55. Mancini, G. et al. Synergistic effects of habitat fragmentation and hunting on the
830 extinction risk of neotropical primates. *Biodivers. Conserv.* **32**, 2655–2669 (2023).
- 831 56. Sze, J. S., Childs, D. Z., Carrasco, L. R. & Edwards, D. P. Indigenous lands in
832 protected areas have high forest integrity across the tropics. *Curr. Biol.* **32**, 4949–
833 4956.e3 (2022).
- 834 57. Plumptre, A. J. et al. Where Might We Find Ecologically Intact Communities? *Front.*
835 *For. Glob. Change* **4**, (2021).
- 836 58. Mair, L. et al. A metric for spatially explicit contributions to science-based species
837 targets. *Nat. Ecol. Evol.* **5**, 836–844 (2021).
- 838 59. Theobald, D. M. et al. Earth transformed: detailed mapping of global human
839 modification from 1990 to 2017. *Earth Syst. Sci. Data* **12**, 1953–1972 (2020).
- 840 60. Mu, H. et al. A global record of annual terrestrial Human Footprint dataset from
841 2000 to 2018. *Sci. Data* **9**, 176 (2022).

- 842 61. Abraham, A. J. et al. Sodium constraints on megaherbivore communities in Africa.
843 Nat. Ecol. Evol. **10**, 105–116 (2026).
- 844 62. Boyce, D. G. et al. A climate risk index for marine life. Nat. Clim. Change **12**, 854–
845 862 (2022).
- 846 63. Levi, T. et al. Spatial tools for modeling the sustainability of subsistence hunting in
847 tropical forests. Ecol. Appl. **21**, 1802–1818 (2011).
- 848 64. Barychka, T., Mace, G. M. & Purves, D. W. The Madingley general ecosystem
849 model predicts bushmeat yields, species extinction rates and ecosystem-level
850 impacts of bushmeat harvesting. Oikos **130**, 1930–1942 (2021).
- 851 65. Heinrich, S. et al. Where did all the pangolins go? International CITES trade in
852 pangolin species. Glob. Ecol. Conserv. **8**, 241–253 (2016).
- 853 66. Tinsman, J. C. et al. Genomic analyses reveal poaching hotspots and illegal trade in
854 pangolins from Africa to Asia. Science **382**, 1282–1286 (2023).
- 855 67. Emogor, C. A. et al. Pangolin hunting in southeast Nigeria is motivated more by
856 local meat consumption than international demand for scales. Nat. Ecol. Evol. 1–10
857 (2025) doi:10.1038/s41559-025-02734-3.
- 858 68. Tulloch, V. J. et al. Why do we map threats? Linking threat mapping with actions to
859 make better conservation decisions. Front. Ecol. Environ. **13**, 91–99 (2015).
- 860 69. Wyborn, C. & Evans, M. C. Conservation needs to break free from global priority
861 mapping. Nat. Ecol. Evol. **5**, 1322–1324 (2021).
- 862 70. Brashares, J. S., Golden, C. D., Weinbaum, K. Z., Barrett, C. B. & Okello, G. V.
863 Economic and geographic drivers of wildlife consumption in rural Africa. Proc. Natl.
864 Acad. Sci. **108**, 13931–13936 (2011).

- 865 71. Harrison, R. D. et al. Impacts of hunting on tropical forests in Southeast Asia.
866 Conserv. Biol. **30**, 972–981 (2016).
- 867 72. Brodie, J. F. Carbon Costs and Bushmeat Benefits of Hunting in Tropical Forests.
868 Ecol. Econ. **152**, 22–26 (2018).
- 869 73. Pekel, J.-F., Cottam, A., Gorelick, N. & Belward, A. S. High-resolution mapping of
870 global surface water and its long-term changes. Nature **540**, 418–422 (2016).
- 871 74. Bingham, H. C. et al. User Manual for the World Database on Protected Areas and
872 world database on other effective area- based conservation measures: 1.6.
- 873 75. European Commission. Joint Research Centre. Institute for Environment and
874 Sustainability. Travel Time to Major Cities. (Publications Office, LU, 2008).
- 875 76. Weiss, D. J. et al. A global map of travel time to cities to assess inequalities in
876 accessibility in 2015. Nature **553**, 333–336 (2018).
- 877 77. Gilbert, M. et al. Global distribution data for cattle, buffaloes, horses, sheep, goats,
878 pigs, chickens and ducks in 2010. Sci. Data **5**, 180227 (2018).
- 879 78. Chen, J. et al. Global 1 km × 1 km gridded revised real gross domestic product and
880 electricity consumption during 1992–2019 based on calibrated nighttime light data.
881 Sci. Data **9**, 202 (2022).
- 882 79. Kummu, M., Taka, M. & Guillaume, J. H. A. Gridded global datasets for Gross
883 Domestic Product and Human Development Index over 1990–2015. Sci. Data **5**,
884 180004 (2018).
- 885 80. Center For International Earth Science Information Network-CIESIN-Columbia
886 University. Gridded Population of the World, Version 4 (GPWv4): Population
887 Density, Revision 11. Palisades, NY: Socioeconomic Data and Applications Center
888 (SEDAC) <https://doi.org/10.7927/H49C6VHW> (2017).

889 81. Potapov, P. et al. The Global 2000-2020 Land Cover and Land Use Change Dataset
890 Derived From the Landsat Archive: First Results. *Front. Remote Sens.* **3**, (2022).

891 82. Running, S. W. & Zhao, M. Daily GPP and Annual NPP (MOD17A2H/A3H) and Year-
892 end Gap- Filled (MOD17A2HGF/A3HGF) Products NASA Earth Observing System
893 MODIS Land Algorithm (For Collection 6.1).

894 83. Amatulli, G. et al. A suite of global, cross-scale topographic variables for
895 environmental and biodiversity modeling. *Sci. Data* **5**, 180040 (2018).

896 84. Valavi, R., Elith, J., Lahoz-Monfort, J. J. & Guillera-Arroita, G. blockCV: An r
897 package for generating spatially or environmentally separated folds for k-fold cross-
898 validation of species distribution models. *Methods Ecol. Evol.* **10**, 225–232 (2019).

899 85. Siriseriwan, W. Smotefamily: A collection of oversampling techniques for class
900 imbalance problem based on SMOTE. *R Package Version* **1**, 15 (2019).

901 86. Shan, G. Monte Carlo cross-validation for a study with binary outcome and limited
902 sample size. *BMC Med. Inform. Decis. Mak.* **22**, 270 (2022).

903 87. Liaw, A. & Wiener, M. Classification and Regression by randomForest.

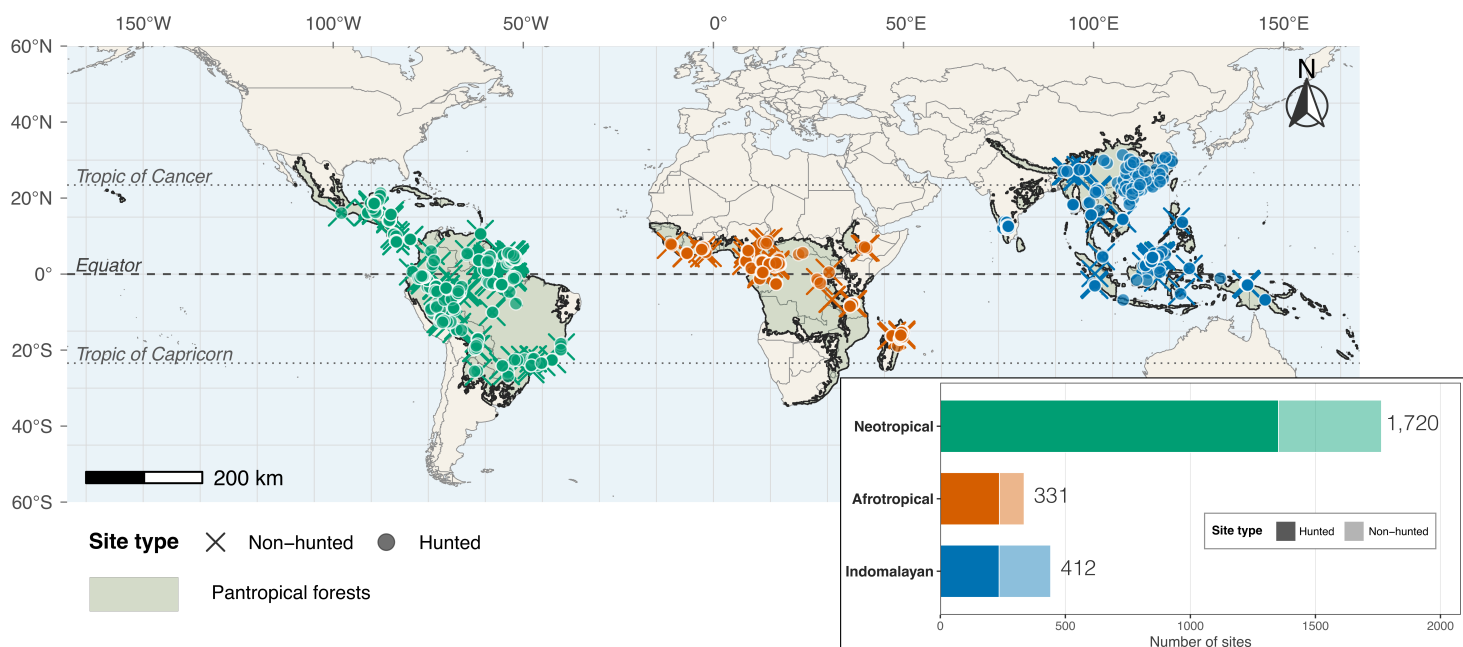
904 88. Dormann, C. F. Calibration of probability predictions from machine-learning and
905 statistical models. *Glob. Ecol. Biogeogr.* **29**, 760–765 (2020).

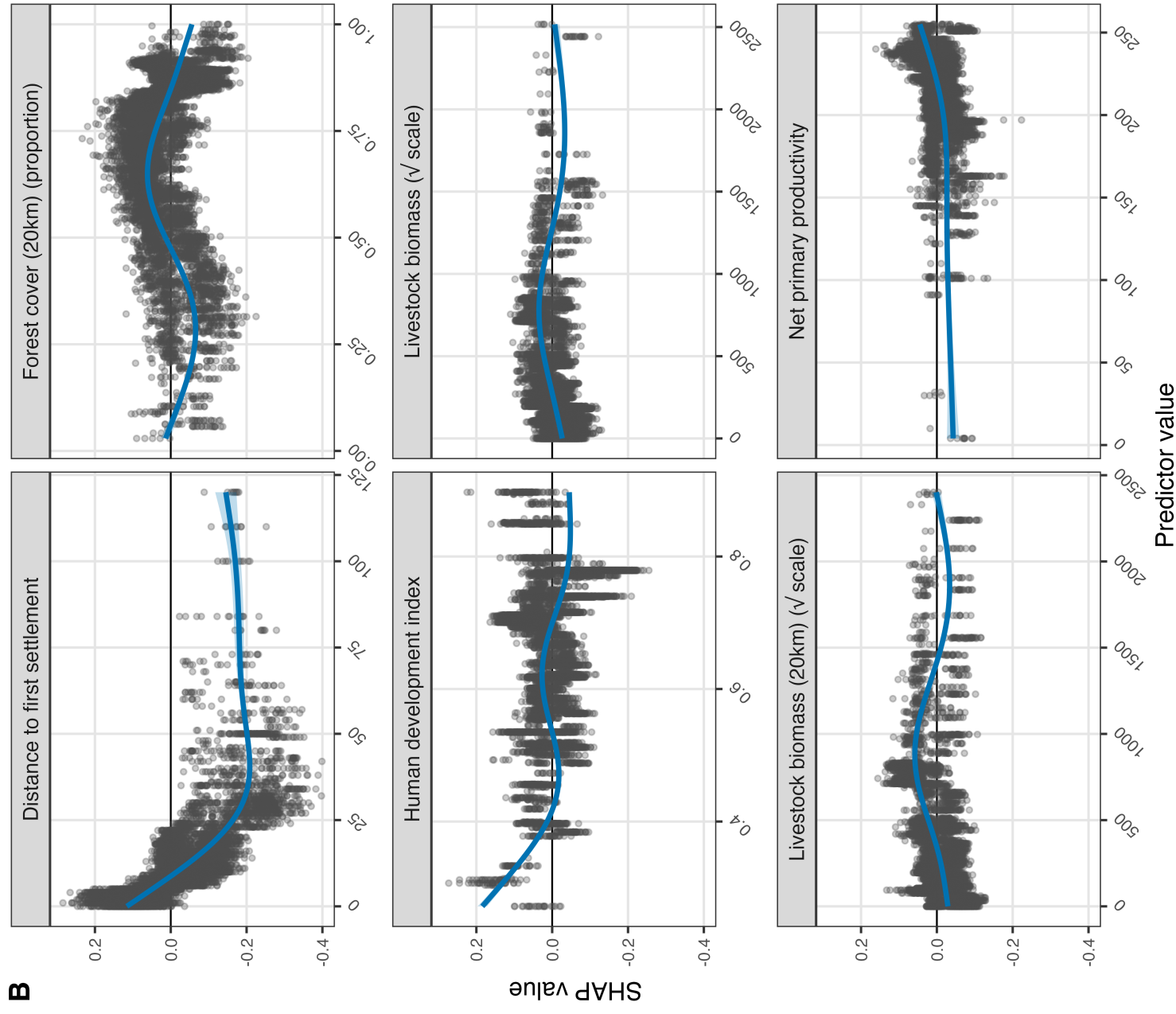
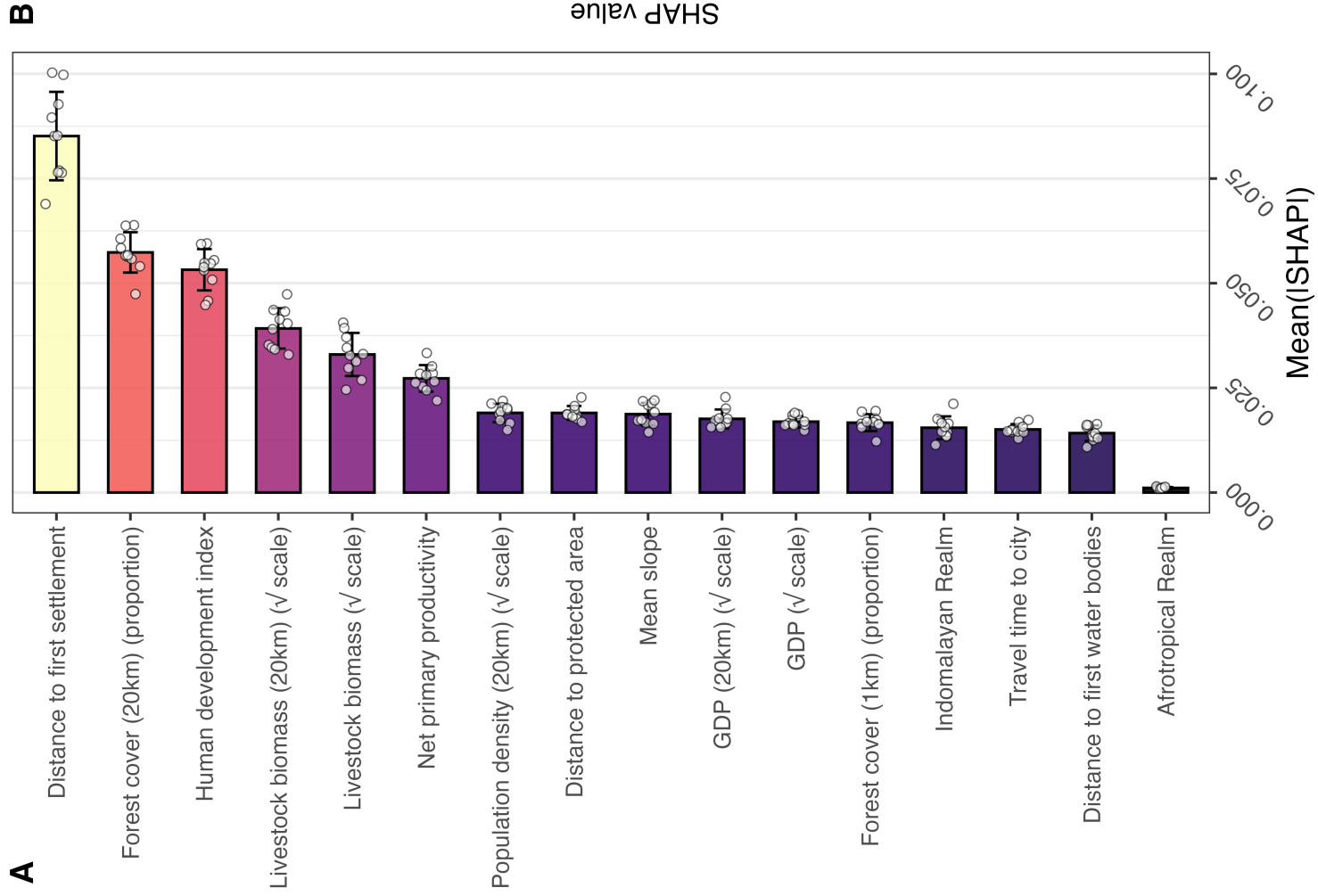
906 89. Mayer, M. shapviz: SHAP Visualizations. 0.9.7
907 <https://doi.org/10.32614/CRAN.package.shapviz> (2022).

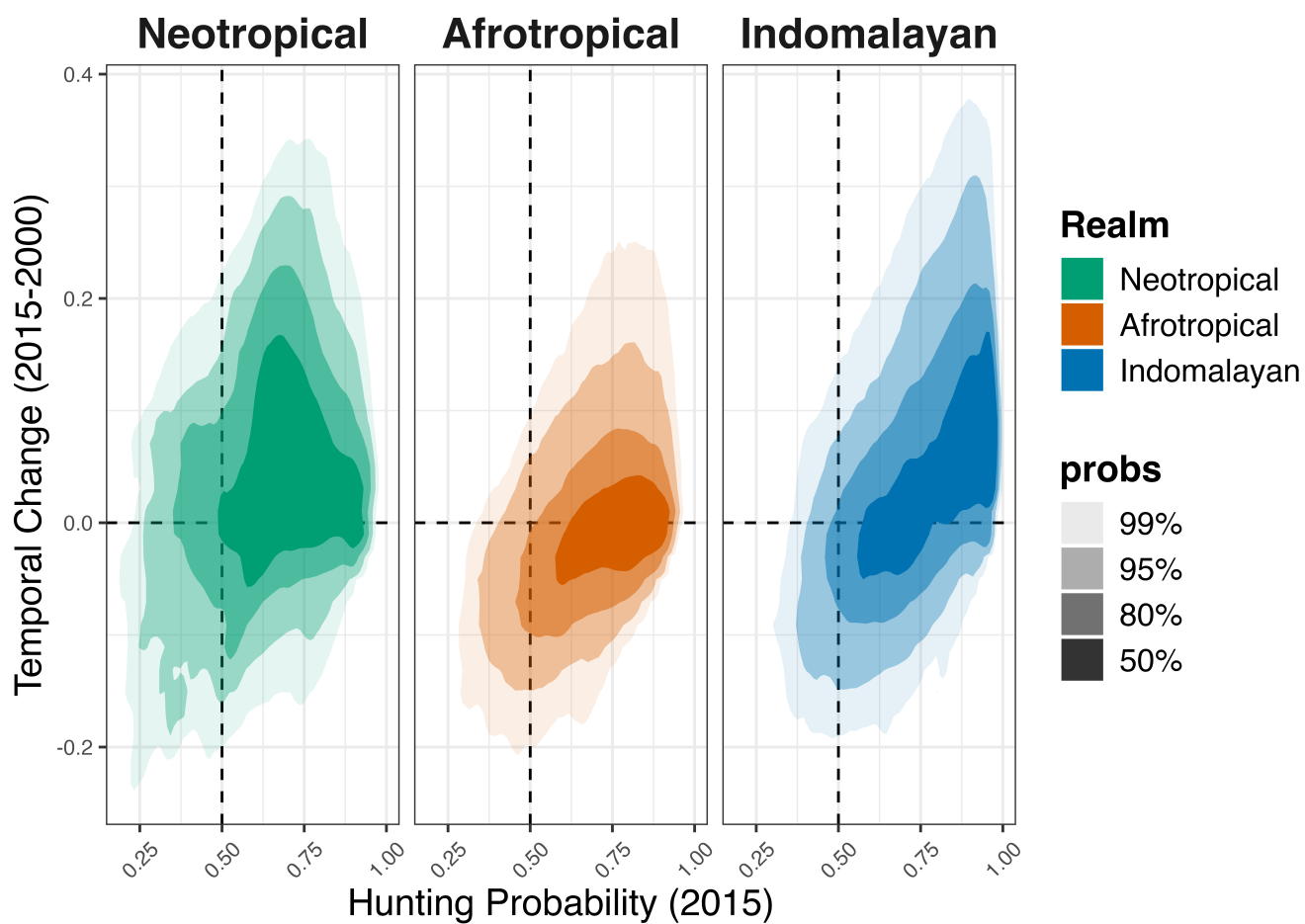
908 90. Marconcini, M., Marconcini, A. M.-, Esch, T. & Gorelick, N. Understanding Current
909 Trends in Global Urbanisation - The World Settlement Footprint Suite. *GIForum*
910 2021 **Volume 9**, 33–38 (2021).

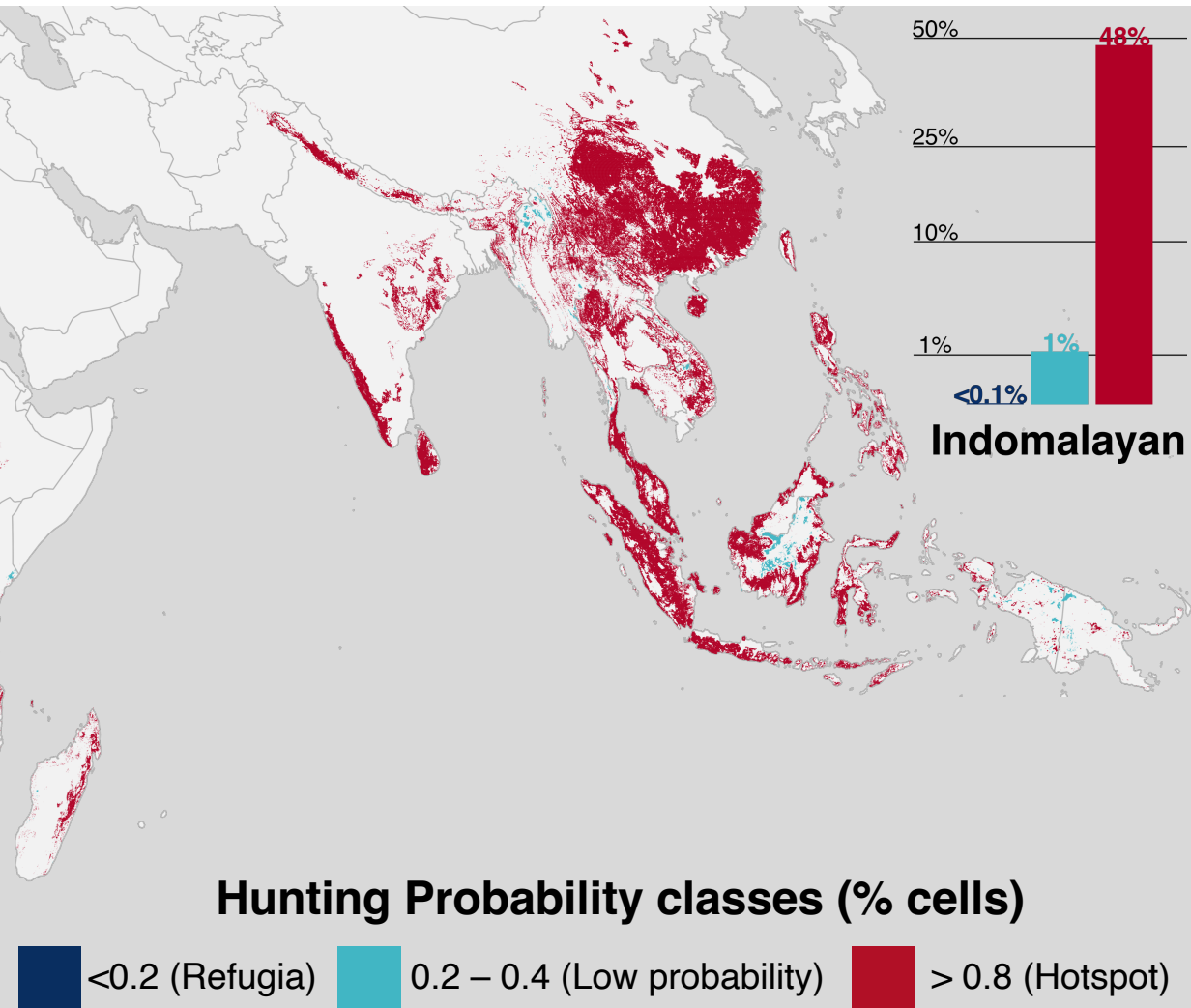
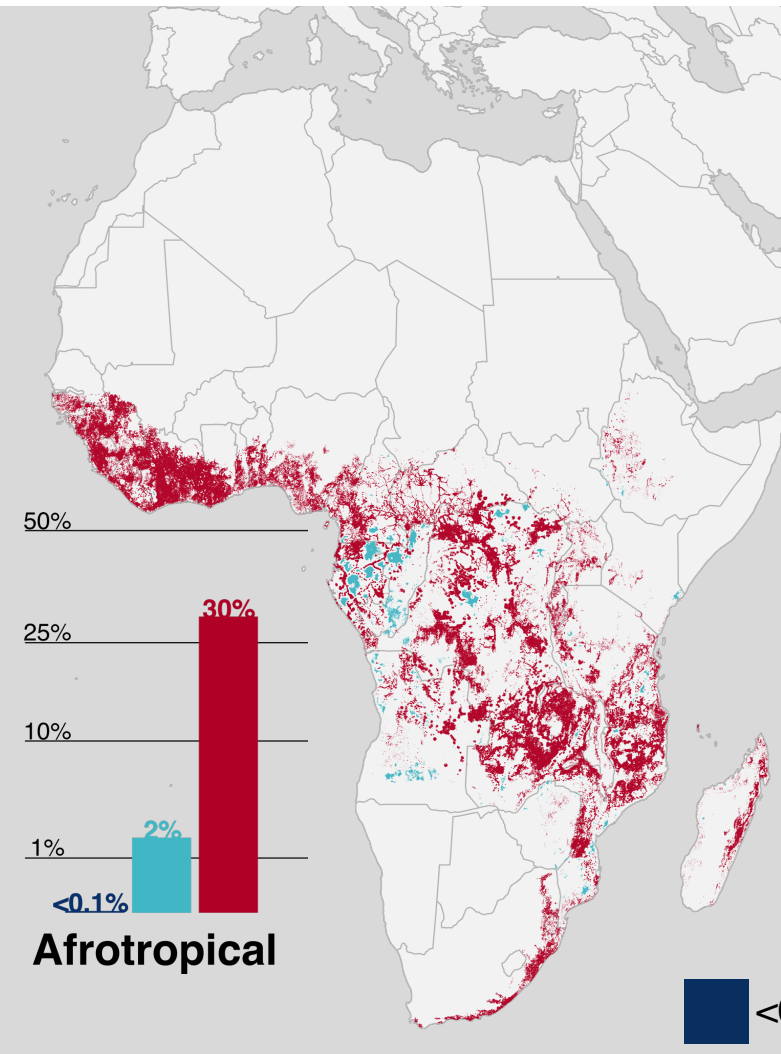
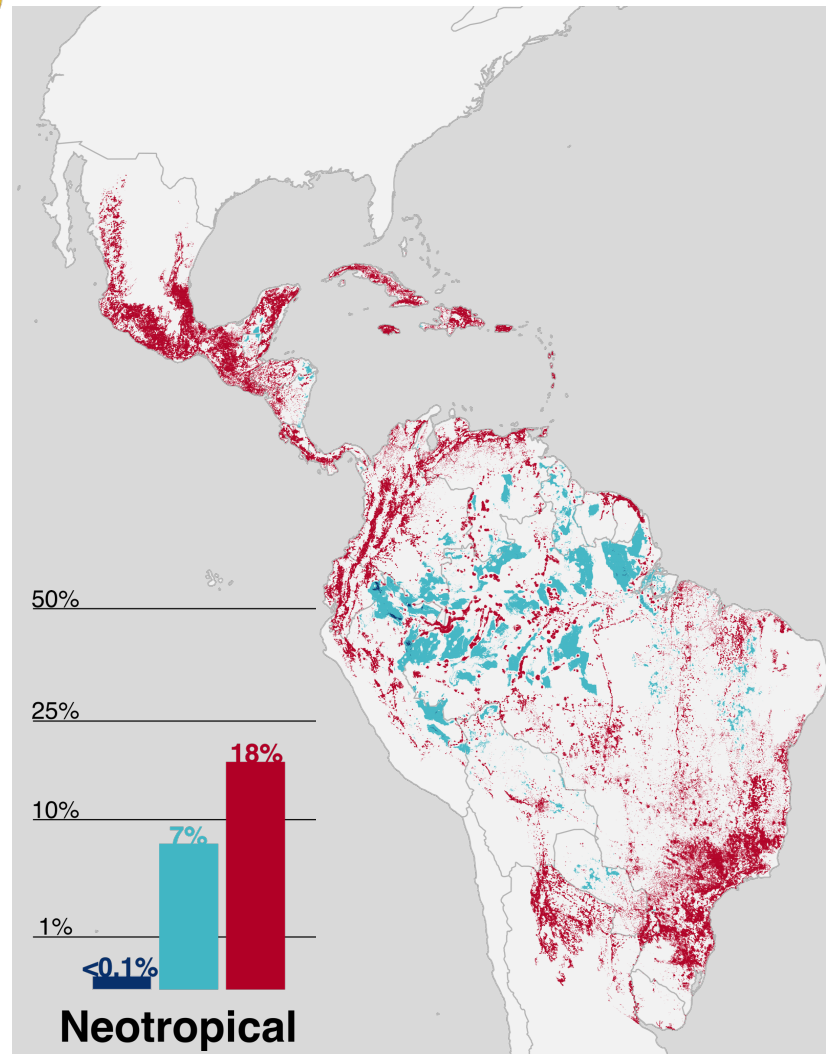
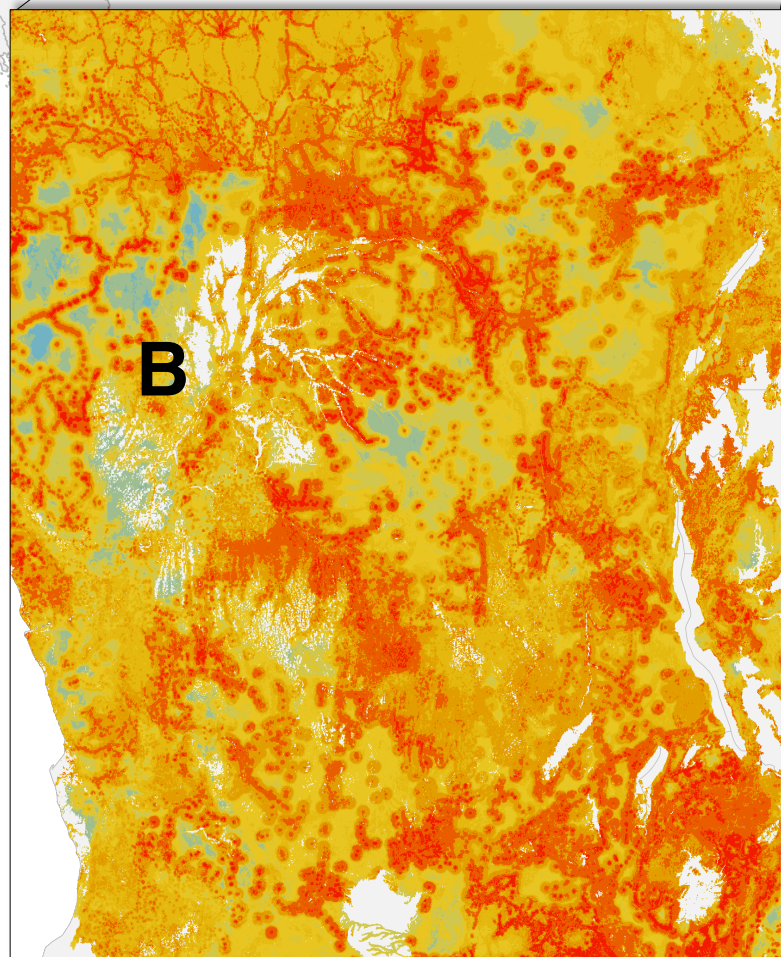
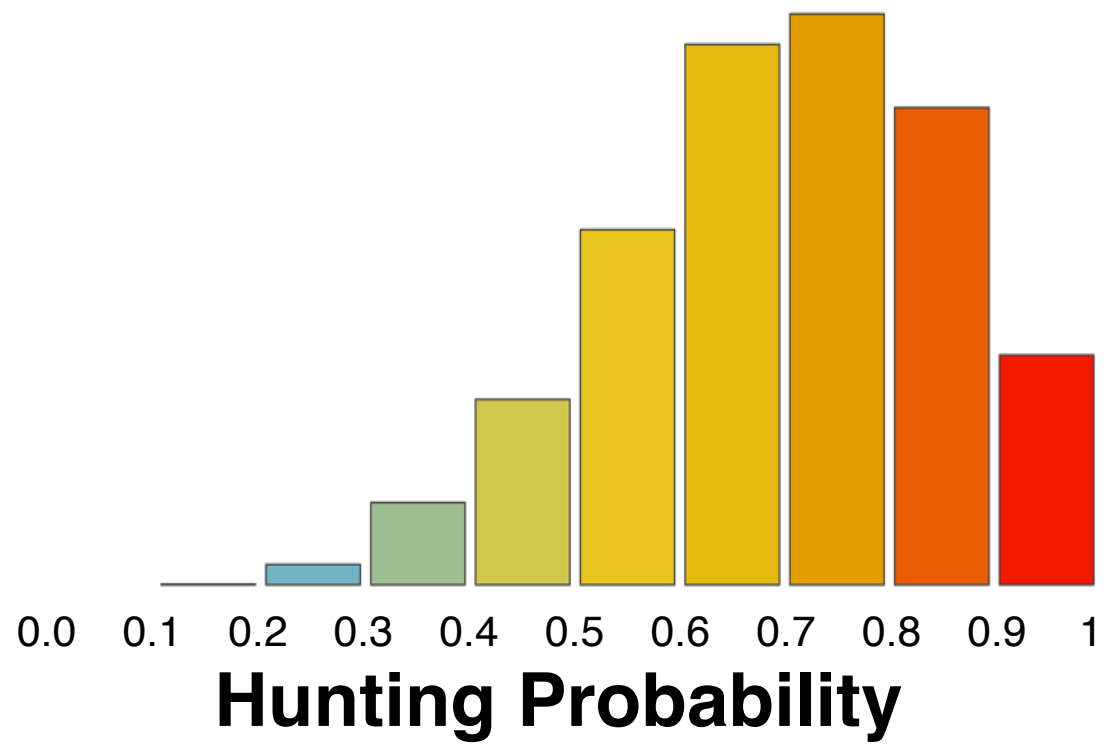
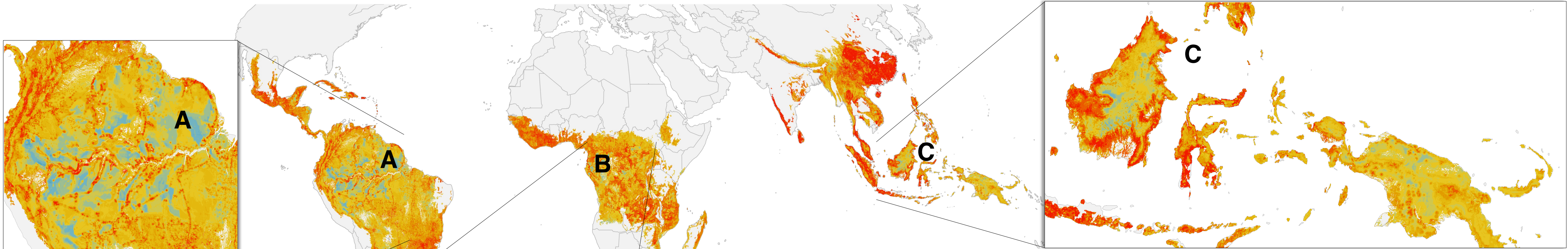
911 91. Massicotte P, South A (2026). *rnaturalearth: World Map Data from Natural Earth*. R
912 package version 1.2, <https://docs.ropensci.org/rnaturalearth/>.

- 913 92. Olson, D. M. et al. Terrestrial Ecoregions of the World: A New Map of Life on Earth:
914 A new global map of terrestrial ecoregions provides an innovative tool for
915 conserving biodiversity. *BioScience* **51**, 933–938 (2001).
- 916 93. Schüßler, D., Rafamantanantsoa, S. M., Ratsimbazafy, J. H., Richter, T. &
917 Radespiel, U. Documentation of commercial and subsistence hunting of Critically
918 Endangered black-and-white ruffed lemurs (*Varecia variegata*) in northeastern
919 Madagascar. *Biodivers. Conserv.* **33**, 221–237 (2024).
- 920

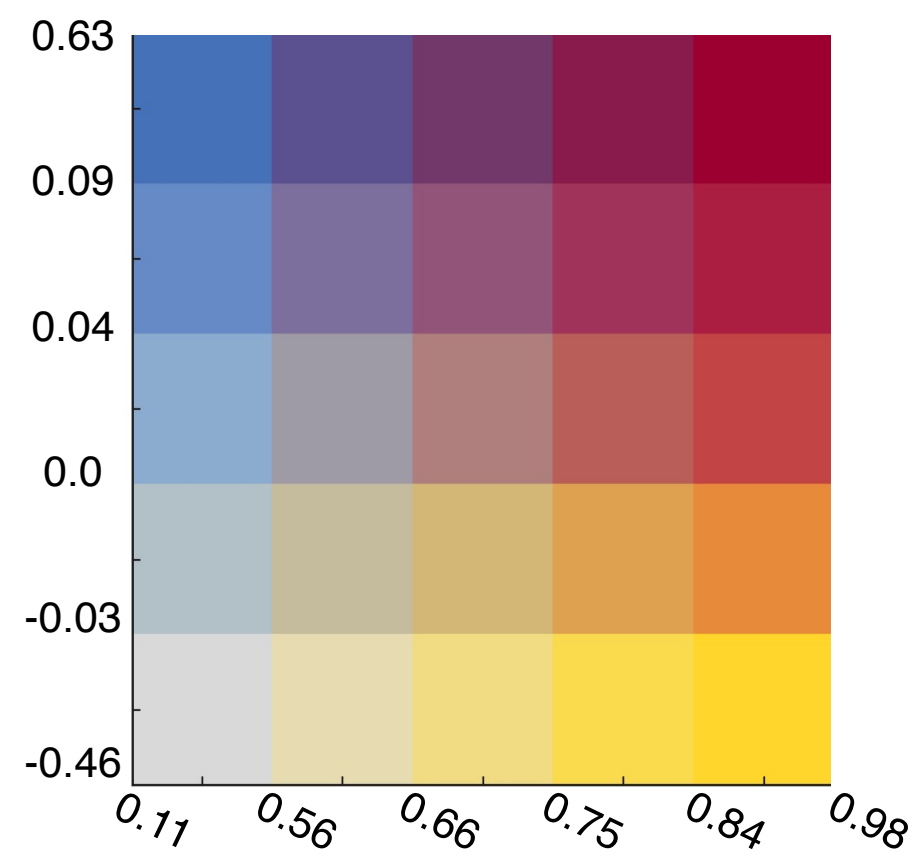








Temporal Change (2015-2000)



Hunting Probability (2015)

