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RESEARCH ARTICLE

Indigenous Peoples' Lands are critical for safeguarding vertebrate diversity across the tropics

Jocelyne S. Sze[1] | **Dylan Z. Childs**[1] | **L. Roman Carrasco**[2] | **Álvaro Fernández-Llamazares**[3,4] | **Stephen T. Garnett**[5] | **David P. Edwards**[1,6]

[1]Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, UK
[2]Department of Biological Sciences, National University of Singapore, Singapore, Singapore
[3]Department of Animal Biology, Plant Biology and Ecology (BABVE-UAB), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain
[4]Institute of Environmental Science and Technology (ICTA-UAB), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain
[5]Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, Northern Territory, Australia
[6]Department of Plant Sciences and Conservation Research Institute, University of Cambridge, Cambridge, UK

Correspondence
Jocelyne S. Sze, Institute of Environmental Science and Technology (ICTA-UAB), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain
Email: jocelyne.sze@gmail.com

Present address
Jocelyne S. Sze, Institute of Environmental Science and Technology (ICTA-UAB), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain

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Abstract

Indigenous Peoples are long-term custodians of their lands, but only recently are their contributions to conservation starting to be recognized in biodiversity policy and practice. Tropical forest loss and degradation are lower in Indigenous lands than unprotected areas, yet the role of Indigenous Peoples' Lands (IPL) in biodiversity conservation has not been properly assessed from regional to global scales. Using species distribution ranges of 11,872 tropical forest-dependent vertebrates to create area of habitat maps, we identified the overlap of these species ranges with IPL and then compared values inside and outside of IPL for species richness, extinction vulnerability, and range-size rarity. Of assessed vertebrates, at least 76.8% had range overlaps with IPL, on average overlapping ~25% of their ranges; at least 120 species were found only within IPL. Species richness within IPL was highest in South America, while IPL in Southeast Asia had highest extinction vulnerability, and IPL in Dominica and New Caledonia were important for range-size rarity. Most countries in the Americas had higher species richness within IPL than outside, whereas most countries in Asia had lower extinction vulnerability scores inside IPL and more countries in Africa and Asia had slightly higher range-size rarity in IPL. Our findings suggest that IPL provide critical support for tropical forest-dependent vertebrates, highlighting the need for greater inclusion of Indigenous Peoples in conservation target-setting and program implementation, and stronger upholding of Indigenous Peoples' rights in conservation policy.

KEYWORDS
area of habitat, extinction vulnerability, forest-dependent vertebrates, Indigenous Peoples' Lands, range-size rarity, species richness, tropical biodiversity

1 | INTRODUCTION

The Kunming-Montreal Global Biodiversity Framework aims to increase the land and sea area under protection to 30% by 2030 (Convention on Biological Diversity, 2022), including Indigenous and traditional territories. The recognition of the integrity and distinct nature of Indigenous and traditional territories to area-based conservation has significance for addressing the historical and ongoing social harms caused by conservation (e.g., land dispossession, violence, and intergenerational trauma) and recognizing the consistency of many Indigenous environmental practices with the Convention on Biological Diversity goals (Reyes-García et al., 2021; Tauli-Corpuz et al., 2020).

Indigenous Peoples' Lands (IPL)—areas which are owned, managed, and/or used by Indigenous Peoples—cover more than a quarter of the Earths' terrestrial surface (Garnett et al., 2018). These areas overlap with 36% of Intact Forest Landscapes (Fa et al., 2020) and are increasingly recognized as critical for global biodiversity maintenance (Brondízio et al., 2021; Reyes-García et al., 2021). At least 25% of tropical forests fall within IPL, where they have reduced deforestation and degradation relative to non-protected areas (non-PAs) and perform similar to PAs (Nolte et al., 2013; Sze, Carrasco, et al., 2022). Possibly arising from a combination of legal protection and Indigenous management, areas of IPL that overlap PAs also have higher forest integrity than non-PAs, suggesting they confer more ecosystem services such as carbon sequestration, water, and climate regulation, while fulfilling important material and non-material needs for Indigenous and local communities and providing habitat for biodiversity (Grantham et al., 2020; Sze, Childs, et al., 2022).

While the case for the global significance of Indigenous stewardship has been developed by Indigenous leaders, scholars, and philosophers for decades, if not longer (e.g., Atleo, 2012; Salmón, 2000), geospatial analysis is increasingly used to quantify the contributions of Indigenous Peoples to global biodiversity conservation. For example, the ranges of many mammal species overlap with IPL, with 2695 (of 4460) species having ≥10% and 1009 species >50% of their ranges on these lands (O'Bryan et al., 2020). In addition, 47% of threatened mammals occur on IPL, and for more than a quarter of them, >50% of their ranges are on these lands (O'Bryan et al., 2020). IPL overlap the ranges of 71% of the world's 521 primate species (Estrada et al., 2022) and support more vertebrate species than existing PAs or randomly selected non-PAs in Australia, Brazil, and Canada (Schuster et al., 2019; see also Corrigan et al., 2018).

Although the relevance of IPL for mammals is apparent, particularly at local to regional scales (Fernández-Llamazares et al., 2021; Renwick et al., 2017), our understanding of the coverage of IPL for other vertebrate taxa at the pantropical level is still very limited. A key question therefore is the degree to which IPL overlap terrestrial tropical vertebrate biodiversity—spanning amphibians, birds, reptiles as well as mammals—and where high values of tropical biodiversity are within IPL globally. Identifying this overlap is key to understanding the various tensions and synergies between current Indigenous environmental practices and global biodiversity conservation efforts underway following the Kunming-Montreal Global Biodiversity Framework.

Focusing on forest-dependent vertebrates of the biodiverse tropics, we examine the importance of IPL for terrestrial biodiversity by tackling three objectives: (1) Identify the extent to which forest-dependent vertebrate area of habitat (AOH) in 2020 overlaps with IPL, PAs, and non-PAs across the tropics; (2) identify countries where IPL contain more species, species at higher risk of extinction, and greater range-size rarity; and (3) quantify whether IPL contain more species, species at higher risk of extinction, and greater range-size rarity than buffer zones outside of IPL.

2 | METHODS

2.1 | AOH for terrestrial tropical forest-dependent vertebrates in 2020

We focused on terrestrial forest-dependent vertebrate groups (amphibians, birds, mammals, and reptiles) that had distributional range maps. Spatial polygons on amphibian, mammal, and reptile distributions were obtained from the IUCN Red List of threatened species (IUCN, 2020) and bird distributions from BirdLife International (BirdLife International, 2020). These maps represent known or inferred areas where species occur based on georeferenced observations and expert knowledge. Following Tracewski et al. (2016), we only considered terrestrial species that were native or re-introduced, and extant or possibly extant. We filtered for species that had any part of their range overlapping tropical forests (Tropical and Subtropical Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests, and Tropical and Subtropical Coniferous Forests biomes; Dinerstein et al., 2017), and whose only preferred habitat was listed as forest for amphibians, mammals, and reptiles, or as having medium or high forest dependency for birds, based on habitat information in the IUCN Red List and BirdLife International, respectively. This yielded 11,872 tropical forest-dependent vertebrates. Tropical forest-dependent vertebrates may also be considered as those that are found exclusively within tropical forests, in addition to forest habitat preferences or dependencies. We thus conducted an additional filter for vertebrates whose distributional ranges were entirely within tropical forest extents; this yielded 1251 vertebrates.

Range distribution maps in equal-area Mollweide projection (ESRI: 54009) were then re-projected to geographic latitude/longitude coordinate system (EPSG: 4326) and rasterized to 1-km^2 pixels to obtain each species' AOH (Brooks et al., 2019). Reductions in AOH contribute to heightened species extinction risk (Durán et al., 2020). To obtain the AOH for each species, we cropped its distribution range to forest cover in 2020 at tropical and subtropical latitudes (each 1-km^2 pixel considered forested if more than half was forested at 25% tree cover threshold; Hansen et al., 2013) and its altitudinal range when available. Species altitudinal limits were obtained from the IUCN Red List and BirdLife International; for amphibians, where altitudinal limits were provided, a 300-m altitudinal buffer on both upper and lower bounds was added, following Ficetola et al. (2014). We used the Global Forest Change dataset for forest cover in 2020 as it covers a larger extent of the tropics compared to the Tropical Moist Forest dataset (Vancutsem et al., 2021).

2.2 | Species ranges within IPL, PAs, and non-PAs

Based on their AOH for 2020, 271 of the 11,872 forest-dependent vertebrates had no remaining suitable tropical habitat left, with 96% of these having small ranges to begin with (i.e., area of distribution <20,000 km^2, which may meet the IUCN Red List Criteria B on geographic range to be listed as Vulnerable). Many of these 271 species were located on small island countries such as Samoa, French Polynesia, Micronesia, and Seychelles, which are not covered by satellite-derived tree cover data (Hansen et al., 2013). For the remaining 11,601 species, we identified species that had some of their range overlapping with mapped IPL (Garnett et al., 2018), PAs (UNEP-WCMC & IUCN, 2020), neither, or both, and calculated the degree of overlap. Areas where IPL (~15.5 million pixels) and PAs (~6.6 million pixels) overlapped (~2.6 million pixels) were labelled as protected Indigenous areas (PIAs). We identified species that were found only in IPL exclusive of the overlapping PIAs to understand the additional contribution of IPL, but kept the overlapping areas for the rest of the analysis, that is, IPL and PAs do not specify mutually exclusive areas and both include the overlapping PIAs. Following O'Bryan et al. (2020), for species that overlapped with IPL, we classified how much of their habitat overlapped at <20%, 20%–40%, 40%–60%, 60%–80%, 80%–99%, and 100% levels.

We used the boundaries of IPL mapped in Garnett et al. (2018), who identified Indigenous lands across 87 countries or politically distinct areas. This dataset represents the most comprehensive assessment of terrestrial lands where Indigenous Peoples have customary ownership, management, and/or governance arrangements in place, regardless of legal recognition. We acknowledge that voids in these maps do not necessarily imply an absence of Indigenous Peoples or their lands, but rather, areas for which an Indigenous connection could not be determined from publicly available geospatial resources. The definition of Indigeneity adopted in this dataset aligns with those of the International Labour Organisation Indigenous and Tribal Peoples Convention 1989 (No. 169) Article 1 (ILO, 1989).

2.3 | Countries where IPL have high values of species richness, extinction vulnerability, and range-size rarity

To identify areas that harbor high numbers of species, highly threatened species, and species with small ranges, we produced maps for species richness, extinction vulnerability, and range-size rarity. For species richness, we stacked the species' AOH maps to obtain the total number of species occurring in a given pixel, for all vertebrates and for each taxon separately.

For extinction vulnerability, we calculated an extinction vulnerability score for each pixel by taking the mean value of the threat score for all species occurring in a given pixel:

$$\text{Extinction vulnerability} = \frac{\sum_{i=1}^{n} T_i}{n}$$

where n = number of species occurring in the given pixel and T = the threat score for the species.

We assigned the following numerical threat scores to each IUCN threat category in a geometric progression, following Wang et al. (2020): Least Concern = 2, Near threatened = 4, Endangered = 8, Vulnerable = 16, and Critically Endangered = 32. For the 1004 species that were data deficient, we obtained predicted threat categories (Bland et al., 2015; Butchart & Bird, 2010; González-del-Pliego et al., 2019; Jetz & Freckleton, 2015). For the remaining 626 species that had no predicted threat category, we calculated the global mean threat score for its taxon, rounded to the nearest integer (i.e., amphibians = 11, birds = 4, mammals = 8, and reptiles = 6). Higher values thus represent pixels containing species in higher threat categories, more vulnerable to extinction.

Range-size rarity highlights areas important for small-ranged species. We calculated range-size rarity as the mean value of the inverse of the AOH for all species occurring in a given pixel:

$$\text{Range-size rarity} = \frac{\sum_{i=1}^{n} \frac{1}{\text{AOH}_i}}{n}$$

where n = number of species in the given pixel and AOH = the number of AOH pixels for the species.

We used the inverse of the species' total AOH (Guerin & Lowe, 2015), instead of calculating the proportion of each species' range within a given pixel, since our maps are at the 1-km^2 resolution rather than 10 or 100 km^2. Higher values thus represent pixels that are more important for species with small ranges.

2.4 | Biological values inside and outside IPL

To compare whether conservation metrics (species richness, extinction vulnerability, and range-size rarity) have higher values inside or outside IPL, we created 10-km radius buffer zones around the IPL. We used 10 km as it is commonly chosen by researchers comparing the effectiveness of PAs with their buffer zones (Fuller et al., 2019). PAs gazetted up to January 2020 were removed from these maps. We opted not to conduct spatial matching to identify counterfactuals for IPL as it is highly improbable to identify (and obtain the data for) all variables contributing to species diversity patterns that might confound with IPL location, which goes beyond accessibility or remoteness of IPL. Furthermore, our intention was not to account for location biases (though we acknowledge that IPL and species are not randomly located) to make comparisons of the effectiveness of IPL in conserving species diversity given similar baseline conditions. Rather, we wanted to examine species diversity as could currently be found within IPL and provided a contrast with their 10-km buffer zones as a comparison for understanding what difference (if any) IPL might make given the varied geographic and historical factors influencing species diversity distribution are likely to be similar between IPL and their 10-km buffers.

We constructed country-level permutation tests on the difference between the mean value of each conservation metric—species richness, extinction vulnerability, and range-size rarity—among IPL and 10-km buffer zones. Null distributions were constructed using 1000 permutations at the pixel level, from which *p*-values were calculated using a two-tailed test (see Supporting Information). This analysis was carried out at the country level (53 countries) to account for possible confounders such as national legislation concerning biodiversity, but note that this does not account for the diversity of ecoregions within each country. IPL cover about 27% of our study area in the tropics, but range between 0.6% and 86.6% for each of the 53 countries where IPL were mapped (Table S1). We present our results following the United Nations geoscheme for geographic regions, covering Africa (*n*=15 countries), the Americas (*n*=21), Asia (*n*=15), and Oceania (*n*=2).

We conducted permutation tests for each of the three metrics—species richness, extinction vulnerability, and range-size rarity. We further plot the biophysical attributes (i.e., slope, elevation, population density, and travel time to nearest city of 5000 inhabitants) associated with IPL and the 10-km buffer zone to understand how such attributes may affect biodiversity. We repeated this analysis using a 50-km radius and all areas outside of IPL for robustness checks.

3 | RESULTS

3.1 | Species' range within IPL, PAs, and non-PAs

Of the 11,601 forest-dependent vertebrate species, 1456 were amphibians, 6398 birds, 1725 mammals, and 2022 reptiles. Of these species, 70% were least concern (*n*=7107 species) or near threatened (977), 9% were data deficient (1004), and the remaining 21% were considered threatened (total=2513; vulnerable=1003, endangered=1026, critically endangered=484). Distributional ranges of 8874 vertebrate species (76.5%) intersected with IPL, encompassing at least 48% of amphibians, 87% of birds, 76% of mammals, and 63% of reptiles.

Nearly all (94.5% or *n*=10,965 species) forest-dependent vertebrates had some of their AOH falling within IPL or PAs, but for 56.6% of them (6205), half or more of their range was outside IPL and PAs (Figure 1a). The mean average value of range overlap in IPL was 23.1% for amphibians, 28.7% for birds, 30.1% for mammals, and 26.7% for reptiles, compared to 51.8%, 57.1%, 53.3%, and 54.1% overlap in areas outside of IPL and PAs for the four taxon groups, respectively. The mean range overlap in PAs was similar to IPL for reptiles at 26%, higher for amphibians at 33.5%, and lower for birds and mammals at 22.4% and 25.9%, respectively. These range overlap values for both IPL and PAs include where they overlap each other (PIAs), which were 8.4% for amphibians, 8.2% for birds, 9.3% for mammals, and 6.8% for reptiles. Similarly, for threatened species (Figure 1b), the mean range

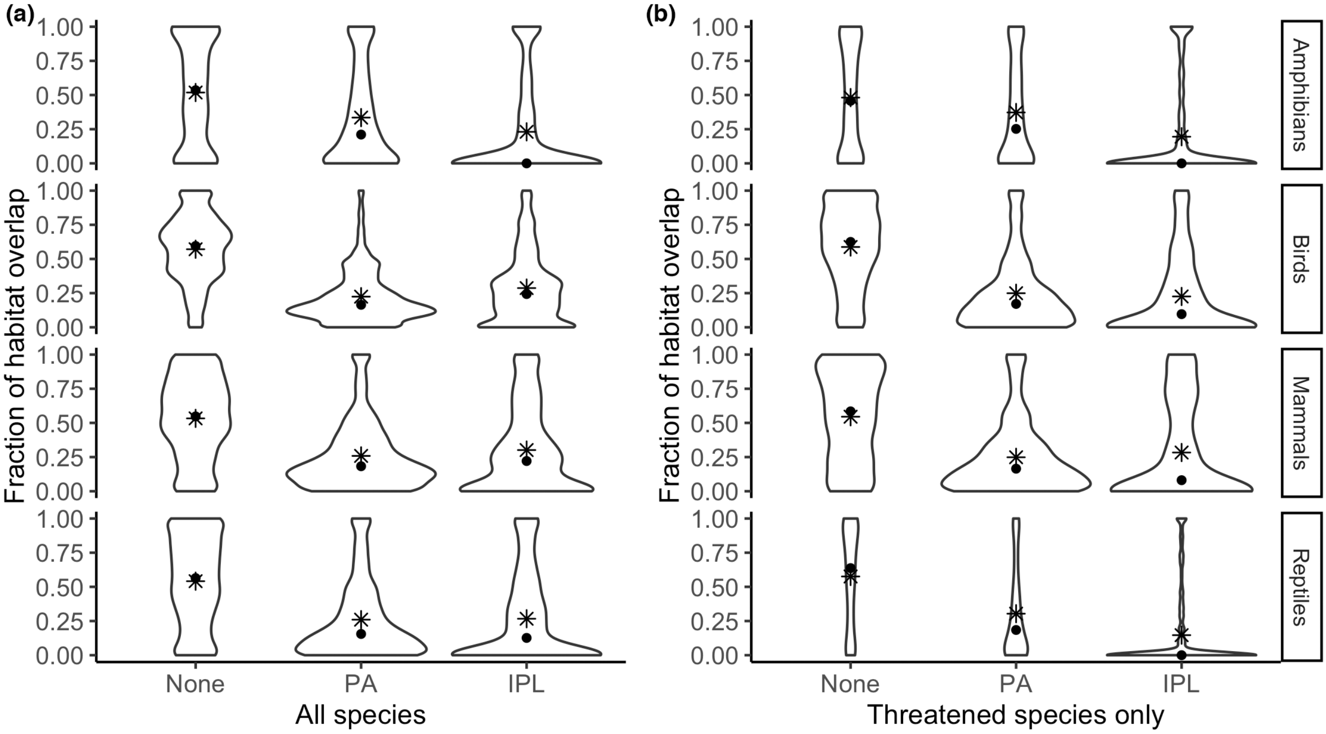

FIGURE 1 Fraction of area of habitat overlap for (a) all amphibians, birds, mammals, and reptiles, and (b) threatened amphibians, birds, mammals, and reptiles, with areas outside both Indigenous Peoples' Lands (IPL) and protected areas (None), protected areas (PAs), and IPL. Mean values represented by the asterisk symbol and median values represented by the filled circle. Note that values for PAs and IPL include where they overlap each other.

overlap in IPL (14.7%–28.3% for the four taxa) was less than that in areas outside IPL and PAs (48.1%–58.8% for the four taxa). However, the mean range overlap in PAs (24.9%–37.2% for the four taxa) was greater than in IPL for amphibians, birds, and reptiles.

Following Hanson et al. (2020), we considered a variable value of coverage of species' AOH as "sufficiently protected," ranging from 100% for AOH <1000 km^2 to 10% for AOH >250,000 km^2 with the coverage value log-linearly interpolated for intermediate AOH (no species had coverage >10,000,000 km^2; Hanson et al., 2023). Given this variable coverage value, 31.3% of the assessed species (*n* = 3633 species) would be considered sufficiently protected by PAs alone, and 42.5% (4935) by IPL alone. This increases to 54.8% (6361) when both PAs and IPL are considered. A total of 2728 species (42.9% of the 6361 species) would not be considered sufficiently protected without the additional coverage provided by IPL. Although we use the terms "sufficiently protected" here as a heuristic, we do not imply that these variable values should be used as targets nor do we imply that IPL automatically confer protection on species. We provide this analysis merely as an illustration of the potential substantial contribution that IPL would provide to species' habitat, especially if Indigenous peoples autonomously chose to partake in national conservation planning, and were supported and included in relevant processes.

Although 51.8%–62.4% of species within each vertebrate taxon had half or more of their range outside IPL and PAs, 120 species were found only within IPL (exclusive of overlap with PAs), 148 species only within PAs (exclusive of overlap with IPL), and 52 species only within the overlapping areas of IPL and PAs (Figure 2a). Of the 120 species found only within IPL, 53 were amphibians, 6 birds, 18 mammals, and 43 reptiles, and nearly half (*n* = 57) of the 120 species were listed as threatened.

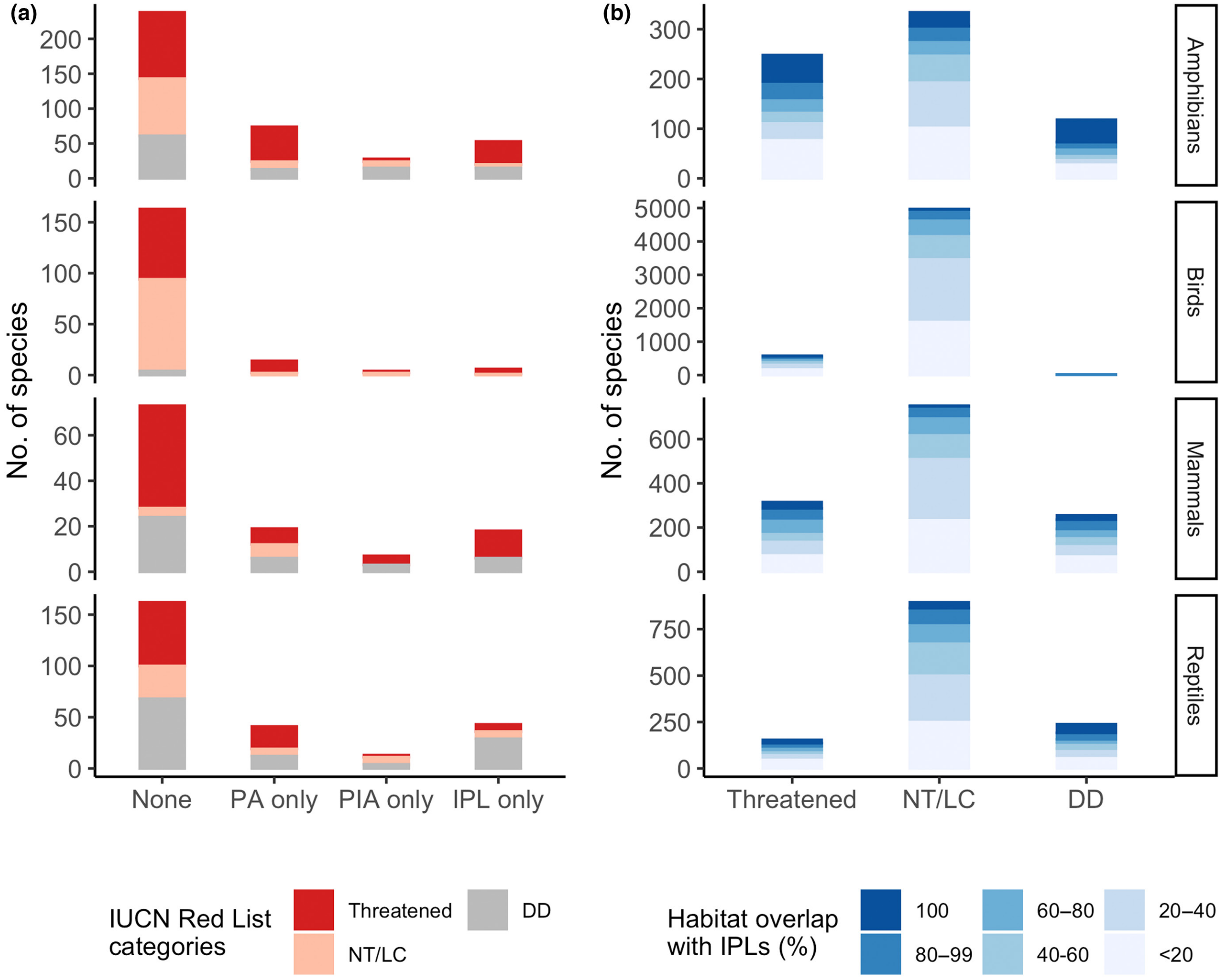

FIGURE 2 (a) Number of species of threatened (critically endangered, endangered, and vulnerable), near threatened/least concern (NT/LC), and data deficient (DD) amphibians, birds, mammals, and reptiles (from top to bottom) completely outside of both Indigenous Peoples' Lands (IPL) and protected areas (None), with all of their range within protected areas (PAs), excluding overlapping protected Indigenous area (PIA) (PA only), with all of their range within the overlap of PAs and IPL (PIA only), and with all of their range within IPL, excluding overlapping PIA (IPL only). (b) Number of species of amphibians, birds, mammals, and reptiles (from top to bottom) with varying % of their range in IPL which are threatened (critically endangered, endangered, and vulnerable), or NT/LC, or DD.

Focusing on the 8874 species whose ranges intersected with IPL (including areas overlapping PAs), while 729 were classified as near threatened and 6221 as least concern, 35.4% of the 700 amphibian species, 10.4% of 5567 birds, 23.8% of 1321 mammals, and 12% of 1286 reptiles were threatened (Figure 2b). About 20% (*n* = 1823) of overlapping species had >60% of their range within IPL (261 amphibians, 855 birds, 347 mammals, and 360 reptiles), of which 42.5% of amphibians, 13.6% of birds, 38.3% of mammals, and 15% of reptiles were threatened. For 288 species, all of their remaining areas of habitat range fell within IPL, encompassing 124 amphibians, 24 birds, 47 mammals, and 93 reptiles. About half of these species in each vertebrate class were threatened, with the exception of reptiles, where most were classified as data deficient. Many data deficient species are, however, likely to be threatened with extinction (Borgelt et al., 2022).

For vertebrate species whose entire range fell within tropical forest extents, 1135 species had remaining AOH in 2020, of which 45.6% were amphibians, 15.4% birds, 15.8% mammals, and 23.3% reptiles (Supporting Information). Threatened species comprised 45.6% of these species, while 27.9% were data deficient and the rest near threatened/least concern. This is quite different to the wider subset of forest-dependent vertebrates, where 21% were considered threatened and 9% data deficient. Given that these 1135 species have their ranges only within tropical forest extents, it is unsurprising that a greater percentage of them would have smaller ranges and greater reliance on diminishing tropical forest habitats, increasing the likelihood that they would be categorized as threatened. Furthermore, 45.6% of these 1135 species were amphibians which are the group of vertebrates with the most data deficient species, contributing to the much higher percentage of data deficient in this subset of entirely forest-dependent vertebrates. The mean average value of range overlap in IPL for these 1135 species was 22.5% for amphibians, 30.3% for birds, 34% for mammals, and 28.7% for reptiles (Figure S1). Although 494 species had some of their ranges overlapping IPL, 76 were found only within IPL (exclusive of overlap with PAs). Of these 494 species, 271 of them have >60% of their range within IPL (Figure S2).

3.2 | Countries where IPL have high values of species richness, extinction vulnerability, and range-size rarity

Across the tropics, median species richness for IPL was highest in South America (Figure 3a), particularly Ecuador and Peru. Within each region, IPL with the highest median species richness were in Gabon and the Republic of Congo for Africa, and Malaysia and Laos

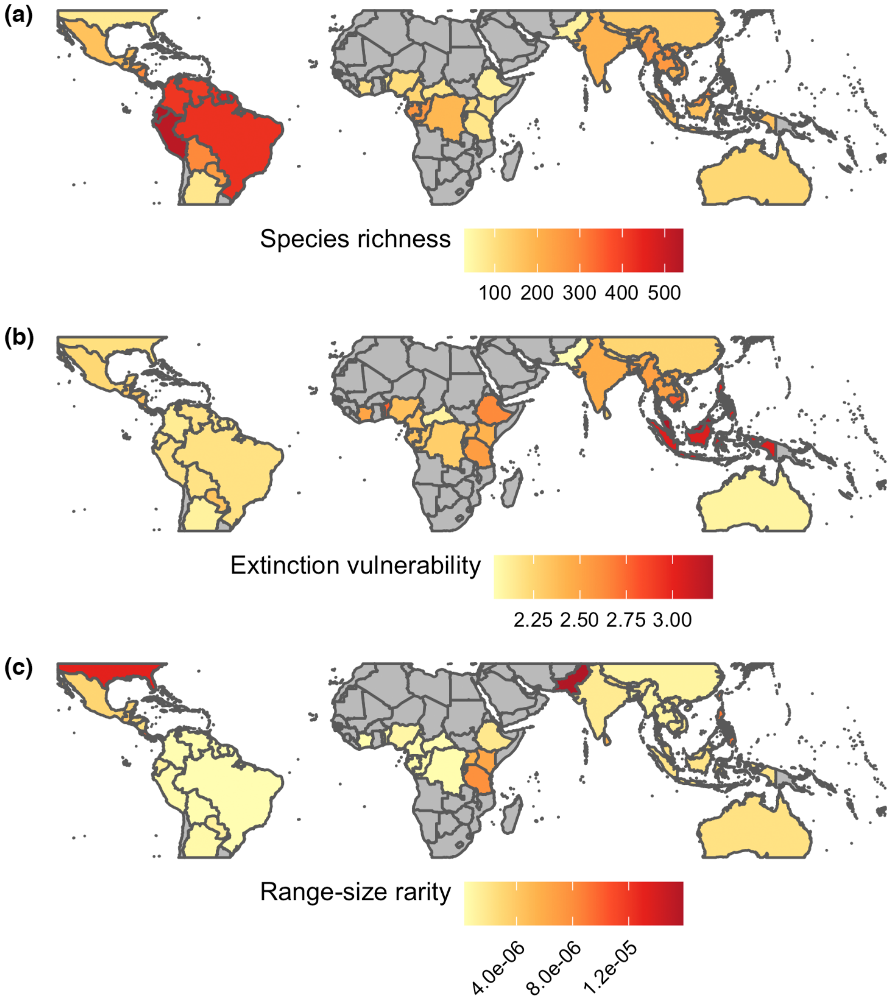

FIGURE 3 Median values of (a) species richness, (b) extinction vulnerability, and (c) range-size rarity in Indigenous Peoples' Lands within tropical and subtropical forest biomes. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

for Asia (Table S2). IPL with species more vulnerable to extinction were concentrated in Southeast Asia, in particular Malaysia and Indonesia (Figure 3b). In Africa, extinction vulnerability was high in Togo and Benin, and in the Americas, it was Costa Rica and Paraguay. IPL with higher values of range-size rarity—areas important for small-ranged species—were concentrated in the small island nations of Dominica and New Caledonia (Figure 3c; though not clearly visible at the pan-tropical scale). In Africa, Rwanda and Tanzania had the highest range-size rarity, while in Asia, Pakistan and the Philippines had the highest range-size rarity. We note that the results for Pakistan was due to *Dendrocopos assimilis*, which although mostly found in non-forested Desert and Xeric Shrublands, has a small overlap with Tropical and Subtropical Coniferous Forests, thus appearing to have only 85 km^2 of suitable forest remaining in 2020; however, this was the only case; thus, we believe our overall results and conclusions are robust. For the subset of species whose entire range was within tropical forests, IPL with high species richness were in French Guiana, Guyana, and Suriname, high extinction vulnerability in Gabon and Republic of Congo, and range-size rarity in Taiwan and Costa Rica (Figure S3; see Supporting Information). We also plot the three metric values together to illustrate how each country scored relative to other metrics for the full set of species (Figure S4).

3.3 | Biological values inside and outside IPL

Of the 53 tropical countries with IPL, 27 had significantly higher forest-dependent vertebrate species richness in IPL than in the 10-km buffer zone outside, while 26 had significantly lower species richness (Figure 4). Countries with higher species richness in IPL were mostly in the Americas and Asia, while those with lower species richness were mostly in Africa and Oceania. These trends were similar for 50-km buffer zone areas and for all areas outside IPL (Figure S5).

Twenty-one countries had more species vulnerable to extinction inside IPL than in the 10-km buffer zone outside, while 31 had lower extinction vulnerability inside IPL. Countries with higher species' extinction vulnerability were mostly in the Americas and Africa whereas Asia and Oceania countries mostly had lower extinction vulnerability risk inside IPL. Differences in range-size rarity inside and outside IPL were small, except for Dominica and United States (not plotted) which had much lower range-size rarity values inside IPL than in the 10-km buffer zone. Twenty-one countries had significantly higher values inside IPL than outside and 28 countries had lower range-size rarity inside IPL. Most countries in Asia had higher range-size rarity values in IPL, while those in the Americas and Africa had mostly lower range-size rarity values in IPL.

Most of these differences between the mean value in IPL and 10-km buffer zone for species richness were driven by birds—as the most speciose group—as well as mammals and reptiles (Figure S6). For some countries where overall species richness was significantly lower inside IPL than outside, such as French Guiana, Costa Rica, Uganda, Rwanda, Philippines, Taiwan, Malaysia, and Australia, amphibian species richness was actually greater inside IPL. Ecuador also had a much higher amphibian species richness inside IPL than outside, compared to all the other countries.

For extinction vulnerability (Figure S7), most of the overall pattern was driven by birds and mammals. Although the overall extinction vulnerability score in IPL was lower than the 10-km buffer zone for almost all Asian countries, except for Laos and Taiwan, at the taxon level, Malaysia, India, Cambodia, Philippines, Indonesia, and Thailand had higher amphibian extinction vulnerability scores inside IPL. India and Nepal also had higher mammalian scores inside IPL, and Malaysia, Indonesia, Nepal, Thailand, and Vietnam had higher reptilian scores inside IPL.

Most of the overall pattern for range-size rarity was also driven by birds (Figure S8). However, while for most taxa differences in values inside IPL and in the 10-km buffer zone were small, for reptiles in Dominica and mammals in Burundi, Rwanda, Uganda, Kenya, Philippines, Nepal, and Australia, IPL had higher range-size rarity values, meaning they were important for smaller ranged animals.

We examined how biophysical variables that act as proxies for land-use frequency (slope, elevation, population density, and travel time) were associated with IPL and the 10-km buffer zone (Figure S9). We found that the mean difference inside and outside IPL for elevation and slope was scattered around 0. For population density, mean differences were generally 0 or negative, indicating similar or lower average population densities in IPL. For travel time, countries in the Americas had mean difference values ranging from −3485 to 5043, while countries in Africa and Asia were generally 0 or negative.

Overall, species richness was highest in IPL in countries in the Americas, where it was significantly higher than in the 10-km buffer zone. Extinction vulnerability of species in IPL was highest in countries in Asia, but this tended to still be significantly less than in the 10-km buffer zone. However, half of American and African countries had species with significantly higher extinction vulnerability in IPL than outside. Range-size rarity of species in IPL was highest for small island nations, with Costa Rica and Pakistan showing significantly higher range-size rarity inside IPL.

4 | DISCUSSION

4.1 | Forest-dependent vertebrates' AOH within IPL

Although IPL cover 28.2% of remaining tropical forest, they provide habitat for about 75% of the vertebrate diversity we assessed. These species may be benefiting from the relatively undisturbed forest habitats retained within IPL (Estrada et al., 2022). Botanical, archaeological and ethnoecological research have shown that Indigenous communities have shaped tropical forests' structure and composition over millennia through their cultural practices (Levis et al., 2017; Maezumi et al., 2018). It is plausible that these practices might have increased landscape heterogeneity and created highly suitable habitats for many vertebrate species (Fernández-Llamazares et al., 2021).

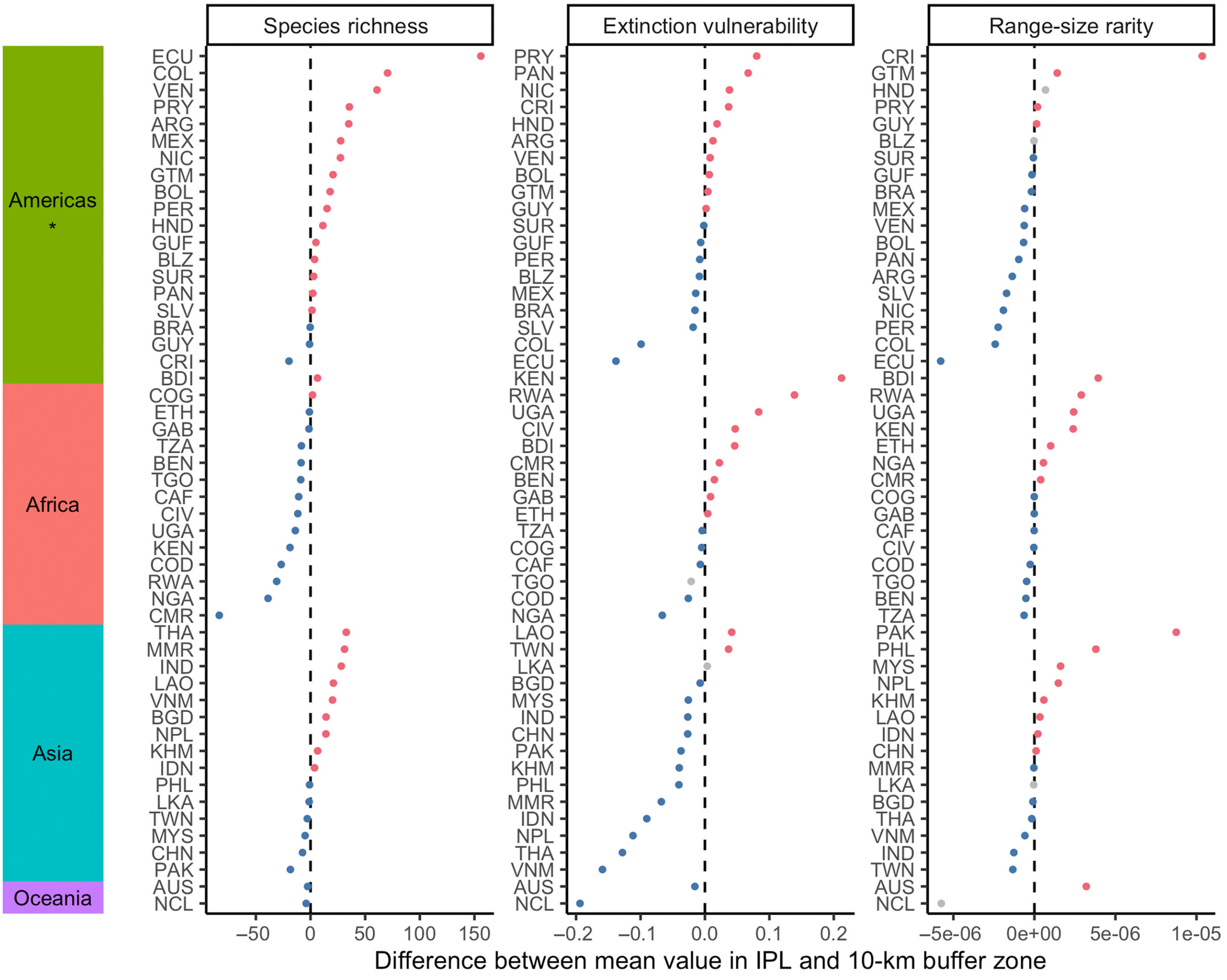

FIGURE 4 Difference between mean values of species richness, extinction vulnerability, and range-size rarity within Indigenous Peoples' lands (IPL) and the 10-km buffer area outside. Red dots represent significantly positive difference (greater value inside IPL), blue dots represent significantly negative difference (smaller value inside IPL), and gray dots represent no significant difference, at $\alpha = .05$ level. *DMA (Dominica) and USA are not plotted here for visual purposes as outliers; DMA values for species richness = −1.77 (sig. neg.), extinction risk = −0.113 (sig. neg.), range-size rarity = −0.00005 (not sig.); USA values for species richness = 50.9 (sig. pos.), extinction risk = −1.88 (sig. neg.), range-size rarity = −0.000334 (sig. neg.). Please see Table S1 for full country names that correspond with the ISO 3166-1 alpha-3 country codes shown in this figure.

For 23.5% of tropical forest-dependent vertebrates, IPL provide additional habitat to PAs that would mean a variable coverage of their AOH fall within IPL or PAs. For example, Giant muntjac (*Muntiacus vuquangensis*) from the Annamite mountain ranges of Laos, Vietnam, and Cambodia has about 24% of its range within PAs, but 72% lies within IPL. While habitat loss and local hunting have contributed to its population decline (Pin et al., 2022), conservation efforts with local communities may reverse the trend.

For 288 species, IPL are critical for their survival, containing their entire range. Ixtlan deer mouse (*Habromys ixtlani*) and small-ranged salamanders *Pseudoeurycea saltator*, *P. smithi*, and *Thorius arboreus* are all endemic to the Sierra de Juarez range of Oaxaca, Mexico. Although few designated state PAs exist in this cloud forest, the Indigenous Zapotec and Chinantec communities have come together to manage their forests collectively and operate a reportedly successful example of community forestry (Chapela, 2005). Such cases demonstrate the existing contributions of Indigenous Peoples and their interwoven knowledge systems and cultural practices to biodiversity conservation efforts. However, this can be contingent on whether lands marked as Indigenous are truly within Indigenous Peoples' ownership, management, and autonomy. Rhaegal's false garden lizard (*Pseudocalotes rhaegal*), endemic to the Cameron Highlands, Malaysia, for example, has its entire global range within IPL. However, Cameron Highlands is a well-known tourist destination and the Indigenous Semai population has limited decision-making influence and power around the development and management of the land (Ismail et al., 2021), with the species' habitat threatened by expanding agriculture and urban settlements (How Jin Aik et al., 2021). In contrast, reduced forest loss in Oaxaca, Mexico, is attributed to the autonomous Indigenous municipalities that retain meaningful influence on local institutions, compared to neighboring municipalities with Indigenous areas but without capacity (Haines, 2021).

Even where territories are recognized as under Indigenous ownership or management and protected legally, this often does not prevent exploitation of their lands by external actors (Quijano Vallejos et al., 2020). For example, Santa Marta wren (*Troglodytes monticola*), which is endemic to the Sierra Nevada de Santa Marta in Colombia, is subjected to many industrial development and extractive pressures, such as mining, illicit crops, and unsustainable agricultural intensification. Despite technically being co-managed with the Tayrona Indigenous Confederation representing the Indigenous Kogi, Wiwa, Arhuaco and Kankuamo communities, and demands from them for the area to be free from mining, there has been a lack of enforcement on environmental protection policies (Duran-Izquierdo & Olivero-Verbel, 2021). Having autonomy over land management, supportive policies, and enforcement of these policies is often critical for enabling biodiversity conservation in IPL. This is particularly pertinent as many countries around the world ramp up their renewable energy transition efforts to mitigate climate change, requiring energy transition minerals and metals that are located on or near lands of Indigenous and peasant peoples (Owen et al., 2022).

4.2 | IPL' importance for forest-dependent vertebrates

Despite IPL covering a relatively small fraction of most species' ranges, they still have high species richness, particularly in the Americas, with 17 countries harboring significantly more species inside than outside IPL (excluding PAs). Ecuador, for example, has much higher species richness inside IPL across all four vertebrate taxon groups. Since our study uses remaining suitable habitat, our finding is likely to be related to higher forest cover retained in IPL, as was discussed in Fernández-Llamazares et al. (2021) for Amazonian bats. Nonetheless, almost all countries in Africa (except Burundi and the Republic of Congo) had lower species richness inside IPL than outside, with Cameroon, in particular, having on average 83.5 species fewer. Overhunting, expansion of logging roads, modern technologies, and influx of farmers have contributed to biodiversity declines, leading to the creation of Community Hunting Zones and PAs by the Cameroonian government, both of which have comparable species richness (Bobo et al., 2014). Since we did not use biodiversity field surveys that might more reliably inform species' presence, and the IPL dataset is not likely to correspond with these Community Hunting Zones, further research on the reasons for a much lower species richness in IPL in Cameroon is needed. Our assessment underscores that a substantial proportion of IPL in Africa face the threat of conversion as extractive industries expand their area of influence (see also Estrada et al., 2022).

Extinction vulnerability of species within tropical IPL was highest in Asia, where species were more likely to be critically endangered than they were in other geographic regions. However, when compared to areas outside IPL, we did not find that species in IPL were more likely to be endangered, except in Laos and Taiwan. Overall, threats to forest-dependent vertebrates are high in Asia since tropical forests have undergone large-scale conversion to rubber or oil palm monoculture plantations (Warren-Thomas et al., 2015; Wilcove & Koh, 2010). Although most IPL in Asia lack official recognition and land tenure security (RRI, 2020), they might still provide refuges for forest-dependent vertebrates. While this is encouraging, climate change could exacerbate the extinction risks of these species, in particular ectothermic amphibians and reptiles (herpetofauna; Mi et al., 2023). While Mi et al. examined the importance of PAs as refuges for herpetofauna under current and future climate scenarios, the additional range coverage of IPL may provide vital buffer for at-risk species.

4.3 | Limitations and conclusion

While the IPL dataset used represents the most comprehensive assessment of terrestrial lands where Indigenous Peoples have customary ownership, management and/or governance arrangements in place, several limitations suggest caution in interpretation. The dataset is based on a particular definition of Indigenous Peoples (see Garnett et al., 2018) and is certainly incomplete as the available maps varied in quality and were likely to have been deficient in countries where publicly available data are limited. However, differences in areas mapped between the IPL dataset of Garnett et al. (2018) and those estimated by Rights and Resources Initiative (2020) as belonging to Indigenous and local communities, which is greatest in Africa (27.7% vs. 69.5% of geographical area, respectively), can be explained by the latter map conflating Indigenous Peoples with Local Communities, a practice now considered undesirable (IIPFCC, 2022).

We used AOH based on species distribution range maps rather than actual presence or absence of species or models based on those. This risks commission errors where species are considered present where they are not, particularly at the relatively high resolution of this study (Di Marco et al., 2017), though we minimized this by identifying forest-dependent species and using recent forest cover to obtain AOH. We also used the Global Forest Change dataset (Hansen et al., 2013) tree cover in 2020 at 50% threshold to determine where tropical forests remain in 2020. This dataset is known to underestimate deforestation and degradation especially at the tropical moist forest extent (Vancutsem et al., 2021), as such our definition of remaining forests in 2020 may be overestimated which correspondingly increases the AOH of forest-dependent vertebrates. Our comparison of IPL with their 10-km buffer zones also did not account for potential localized spillover effects adjacent to IPL, since deforestation leakage from IPL would reduce species' AOH outside of IPL and may thus not present a complete understanding of IPL and their importance for forest-dependent vertebrate diversity. There may also be gaps in the range maps, particularly in IPL, since such areas are often surveyed less well than other lands (dos Santos et al., 2015). Research permits to sample biodiversity in many countries do not include authorization to enter IPL (e.g., Bolivia and Brazil), and legislation controlling access to IPL may be a potential barrier for carrying out conservation-related research there (dos Santos et al., 2015). As such, while we present a comprehensive overview of vertebrate diversity in IPL across the tropics, these data limitations should be taken into consideration.

Future research should thus focus on using survey data alongside ethnographic and participatory methods (Noss & Leny Cuellar, 2008) to better understand species abundance and distributions within IPL, especially of larger bodied species at risk of overhunting. These can help introduce sustainable hunting quotas or community-imposed bans on sensitive species. We focused on four major vertebrate taxa, which are good indicators of patterns in other taxa (Barlow et al., 2007; Edwards et al., 2014). However, there remain many gaps in taxonomic coverage. For example, it would be valuable to know whether IPL are associated with insect diversity given Indigenous peoples' biocultural approaches to pollinator conservation (Hill et al., 2019), the crucial role that insects play in ecosystem functioning (Ewers et al., 2015) and their drastic global declines in diversity and abundance (Forister et al., 2019).

Nonetheless, our findings suggest that IPL and their traditional stewards are critical for maintaining vertebrate biodiversity across the tropics. These results strongly align with those of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services Global Assessment (IPBES, 2019) and other global studies on Indigenous land-based stewardship (ICCA Consortium, 2021). Concerted action to support Indigenous Peoples in securing their lands and recognition of their historical rights to do so is thus inextricably linked to global efforts to combat biodiversity loss.

Our findings can support decision-making of where and how conservation interventions could occur, specifically the kinds of land management or ownership agreements that Indigenous Peoples can negotiate for to contribute to national conservation targets, should they wish to do so (Renwick et al., 2017). Considering that land tenure insecurity is pervasive across much of the tropics (Ceddia et al., 2015; Robinson et al., 2014), granting Indigenous Peoples formal legal title to their lands should be seen as an important mechanism for protecting IPL from encroachment and safeguarding the biodiversity they harbor (Baragwanath & Bayi, 2020; Blackman et al., 2017). Any conservation efforts taking place in IPL must include the participation of Indigenous communities throughout the entire conservation planning process. Recognizing the agency and leadership of Indigenous Peoples as rights-, knowledge-, and stake-holders (beyond consent-giving), and the need for equitable distribution of benefits and compensation for costs are vital to underpin the success of the newly established Kunming-Montreal Global Biodiversity Framework (Reyes-García et al., 2021; Sandbrook et al., 2023).

AUTHOR CONTRIBUTIONS

Jocelyne S. Sze: Conceptualization; data curation; formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **Dylan Z. Childs:** Conceptualization; methodology; supervision; writing – review and editing. **L. Roman Carrasco:** Conceptualization; methodology; supervision; writing – review and editing. **Álvaro Fernández-Llamazares:** Resources; writing – review and editing. **Stephen T. Garnett:** Resources; writing – review and editing. **David P. Edwards:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Amphibian, mammal, and reptile distributions were obtained from the IUCN Red List of Threatened Species (https://www.iucnredlist.org/resources/spatial-data-download), and bird distributions from BirdLife International (http://datazone.birdlife.org/species/requestdis). Original data used for analysis are publicly available or can be requested from the respective authors. All code used in this analysis and the final results datasets used to produce figures are available in Zenodo at http://doi.org/10.5281/zenodo.8385939.

ORCID

Jocelyne S. Sze https://orcid.org/0000-0001-8183-766X
Dylan Z. Childs https://orcid.org/0000-0002-0675-4933
L. Roman Carrasco https://orcid.org/0000-0002-2894-1473
Álvaro Fernández-Llamazares https://orcid.org/0000-0002-7813-0222
Stephen T. Garnett https://orcid.org/0000-0002-0724-7060
David P. Edwards https://orcid.org/0000-0001-8562-3853

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SUPPORTING INFORMATION

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

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