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Patterns of vertebrate richness across global anthromes: prioritizing conservation beyond biomes and ecoregions

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ABSTRACT

There is a clear need to refocus the way we prioritize conservation actions at a global scale to incorporate human systems. Anthromes have been suggested as one tool for integrating anthropogenic effects on ecosystems, but spatially explicit comparisons of biodiversity patterns are limited at a global extent. To address this gap, we used global data sets of anthromes and terrestrial vertebrate richness. We ranked anthromes by richness to all and threatened species at a global scale, temperate and tropical extents, and within major geographic regions. We tested for correlations between overall richness and count of threatened species, between taxonomic groups (birds, mammals, amphibians), and between taxa and conservation actions. At the global scale, there is high variation in vertebrate species richness by anthrome with low species richness in wildlands and higher richness in villages, rangelands, and woodlands. Threatened species distribution follows a similar pattern with high numbers of threatened species in village and remote seminatural woodland anthromes. Analyzes at temperate and tropical extents suggests unique opportunities in different regions, for example when considering the value of land sparing or sharing. There is clear heterogeneity across geographic regions. Richness in anthromes and hotspots are spatially aligned across all taxa but not for threatened taxa. Protection was negatively correlated with threatened bird richness. Human modified ecosystems provide opportunities for conservation and global and regional ranking of anthromes helps identify priorities that can complement biome and ecoregion-based prioritization. Currently, much of conservation research and prioritization is in wildlands or perceived natural landscapes, however this data shows a clear need to focus conservation efforts on seminatural, managed, and residential lands. These data would be helpful for global conservation organizations as an updated framework that can be used to prioritize global resource allocation while considering both ecological and social systems.

1. Introduction

Undesired biodiversity trends persist across ecosystems globally (Butchart et al., 2010) including continued loss of species and decline of populations (e.g., Rosenberg et al., 2019), loss of ecosystems (e.g., Hansen et al., 2013) and continued pressures including habitat fragmentation, pollution, and overexploitation at local and global extents (e.g., Butchart et al., 2010; Williams

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et al., 2020). To better understand drivers of these trends, spatial patterns of global biodiversity, prioritization, and protection have been assessed based on biomes, ecoregions, and other natural systems (e.g., Hoekstra et al., 2005) or on political units (e.g., Chape et al., 2005). These studies of biodiversity and conservation through a traditional lens have revealed important global patterns and changes. For example, Chape et al. (2005) found that the proportion of habitats protected varied greatly both by geographic region and by biome; ranging from 25.6% in Central America down to 7.6% in south Asia and from 23% in tropical moist forest to 5% in cold semidesert. Hoekstra et al. (2005) mapped protection and habitat loss, ranking rates of change by biome and ecoregion finding the conservation risk index score (a ratio of protected and converted land) was highest in temperate grasslands, savannas, and shrublands and lowest in the tundra. Joppa and Pfaff (2009) mapped protected areas by ecoregion and assessed the effectiveness of their placement; finding that protected areas are biased towards landscapes that lack pressure to be converted (e.g., deserts). Focusing on specific taxonomic groups, Tedersoo et al. (2014) found that fungal diversity was greatest in the tropics, but that relative richness of groups varied by biome and biogeographic region. Pimm et al. (2014) demonstrated that the greatest richness of plants was in tropical and Mediterranean ecoregions. Biome and ecoregion frameworks have also been used to model and anticipate future changes. For example, Sala et al. (2000) provided a ranking of biomes with respect to expected ecosystem changes across varying scenarios for the year 2100.

These efforts focused on natural systems are valuable; however, less than 45% of the planet remains wild or even seminatural (Allan et al., 2018). Given the known extent of human change of the landscape (Foley et al., 2005; Ellis and Ramankutty, 2008), such global narratives based on ecological classifications reflecting temperature, precipitation, elevation, and latitude do not provide accurate or actionable representations of biodiversity distributions and change (Ellis et al., 2010; Martin et al., 2014). Thus, there is a clear need for added perspectives that consider how biodiversity varies globally, within both human and natural systems, and the opportunities and challenges associated with that variation. This gap–specifically the lack of global conservation prioritization based on globally representative land use and land cover–needs to be filled. Therefore, in the same way Hoekstra et al. (2005) called for expansion beyond conservation in hotspots toward “entire at-risk ecosystems”, the scale of human land-use change necessitates that we expand the scope of conservation once again to consider conservation on natural, managed, and novel ecosystems at a global scale and integrate human influence into the framework within which we consider patterns of biodiversity loss and conservation success (Martin et al., 2014).

Answering a call for global synthesis of human and natural systems, Ellis and Ramankutty (2008) reclassified terrestrial vegetation to incorporate land-use intensity and human population density. The resulting “anthromes,” or anthropogenic biomes, reflect the extent to which humans have shaped the Earth's surface and offer a succinct and globally representative way to incorporate human systems into conservation and biodiversity assessments (Martin et al., 2014). Anthromes have been used to frame vertebrate biodiversity patterns at local extents for mammals (e.g., Gómez et al. 2018) and birds (e.g., Quinn et al. 2014, Quinn et al. 2017). At a global extent, Ellis et al. (2012) demonstrated that plant species richness was greatest in seminatural remote woodlands, dense mixed settlements, and pastoral villages. Brum et al. (2013) found that land use, specifically anthrome type, was the most important factor in determining the distribution of threatened amphibian species–more so than climate–providing further evidence that land-use change is an essential driver of species richness and distribution. Pekin and Pijanowski (2012) demonstrated the influence of urbanization and high-intensity crop production on the threat status of mammals. To our knowledge, there has not been a global assessment of bird richness at a global scale focusing on anthropogenic biomes and there has not been an inclusive assessment of anthrome focused richness and threat across these vertebrate taxa.

Building on the biome- and anthrome-focused studies discussed above, we evaluated vertebrate species richness of all vertebrate species and threatened vertebrate species across anthromes to prioritize opportunities (all species richness) and challenges (threatened species richness) for three groups of taxa; birds, mammals, and amphibians. Specifically, we ask (1) Which anthromes have the highest vertebrate species richness and which have the highest number of threatened vertebrate species?; (2) How do these patterns vary by region?; (3) Is there a relationship between the distribution of all and threatened species?; and (4) How do protected areas and hotspots correlate with richness?

2. Methods

2.1. Data sources

We obtained global anthrome classification and distribution data for the year 2000 from the Anthromes 12k Discrete Global Grid dataset (Gauthier et al., 2021; Ellis et al., 2021). The Anthromes 12k data are derived via a rule-based classification model of human population density and land use from the HYDE 3.2 dataset, which includes estimates of land cover, irrigation, and rice agriculture for the past 12,000 years (Klein Goldewijk et al., 2017; Ellis et al., 2020). Prior to applying the anthrome classification, the HYDE 3.2 data were regridded to a level-12 Discrete Global Grid system, an equal-area hexagonal tessellation of the Earth’s surface at approximately 10 km resolution (Sahr et al., 2003). Regridding the HYDE data to an equal-area system eliminated areal distortions that would have biased the anthrome classification at higher latitudes. See Ellis et al. (2021) and Gauthier (2021) for more information on the Discrete Global Grid system and its impact on the resulting anthrome estimates.

We obtained vertebrate species richness data–representing the total number of bird, mammal, and amphibian species from BiodiversityMapping.org (Jenkins et al., 2013; Pimm et al., 2014). These data reflect breeding bird ranges from BirdLife International and range data for mammals and amphibians from the International Union for the Conservation of Nature (IUCN). Richness of all species in each taxonomic group was calculated by Jenkins et al. (2013) where for each 10 × 10 km grid cell, any species that overlapped any part of the cell counted as a presence of that species. Threatened species classifications were determined by Jenkins et al. (2013) and Pimm et al. (2014) based on species considered vulnerable, endangered, or critically endangered on the IUCN Red List.

At a global extent, we obtained data on protected areas and hotspots from Martin et al. (2014). In that analysis, they calculated the extent of protected areas and hotspots within anthromes by overlaying the 2010 WDPA area and biodiversity hotspots Myers et al. (2000) respectively and calculating overlay areas for each.

2.2. Data analyzes

We aggregated all species richness layers to the same level-12 Discrete Global Grid system as the anthrome data using zonal statistics, accounting for exact fractional coverages of raster grid cells by the hexagonal polygons (Baston, 2020). We calculated richness by anthrome first at a global extent, then separately across temperate and tropical regions, and across geographic regions (Gauthier, 2021). We tested for patterns and relationships in R (R Core Team, 2020). We used generalized linear models with a Gaussian distribution to test for relationships between richness (all and threatened) and conservation efforts or prioritization proxies. We used Akaike Information Criterion (AIC) model selection to rank the models of prioritization with inference based on 95% confidence intervals.

3. Results

3.1. Global Summary

At a global extent, the median richness of all birds, mammals, and amphibians was greatest in villages, rangelands, and woodlands (Table 1, Fig. 1), though relative ranking of anthromes differed between taxa. Median richness was lowest for each taxon in wild lands. The median number of threatened birds and mammals was the greatest in villages. Median species richness of threatened amphibians is low across anthromes.

3.2. Temperate vs. Tropical

3.2.1. All Species

In the tropics, the median richness of birds, mammals, and amphibians was greatest in remote woodlands and wild woodlands (Fig. 2, Table 2). The median richness of all three taxonomic groups was the next highest in croplands and woodlands. In temperate regions, bird richness was highest in villages and mixed settlements, followed by croplands. Mammal

Table 1
Summary of median and mean richness for all and threatened bird, mammal, and amphibian richness.

Anthrome		Bird				Mammal				Amphibian			
		All		Threatened		All		Threatened		All		Threatened	
Class	Label	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean	Median	Mean
Dense Settlements													
11 Urban		187	216	4	6	47	54	1	2	13	17	0	0
12 Mixed settlements		198	237	4	5	55	64	2	4	17	19	0	1
Villages													
21 Rice villages		249	256	8	9	52	58	4	4	16	16	0	0
22 Irrigated villages		211	219	7	8	47	50	2	3	9	10	0	0
23 Rainfed villages		261	261	7	7	58	67	2	4	14	15	0	0
24 Pastoral villages		279	266	5	6	69	79	3	3	15	19	0	1
Cropland													
31 Residential irrigated croplands		171	197	4	5	49	57	2	3	7	10	0	0
32 Residential rainfed croplands		190	233	4	5	54	66	1	3	12	16	0	0
33 Populated croplands		184	214	4	6	47	57	0	2	8	13	0	0
34 Remote croplands		173	210	3	4	46	54	0	2	8	13	0	0
Rangeland													
41 Residential rangelands		278	263	5	5	71	78	2	3	15	18	0	0
42 Populated rangelands		203	224	5	5	53	66	2	3	7	14	0	0
43 Remote rangelands		156	166	2	3	36	46	1	2	4	9	0	0
Seminatural													
51 Residential woodlands		249	266	4	5	68	78	2	5	17	21	0	1
52 Populated woodlands		255	276	4	5	69	84	2	4	16	24	0	0
53 Remote woodlands		175	259	3	4	45	81	1	3	5	28	0	0
54 Inhahited treeless & barren lands		111	149	3	4	31	46	2	2	2	8	0	0
Wildlands													
61 Wild woodlands		109	144	2	2	33	46	0	1	2	10	0	0
62 Wild treeless & barren lands		42	60	1	2	17	19	1	1	0	1	0	0
63 Ice, uninhabited		11	17	0	1	5	6	1	1	0	0	0	0

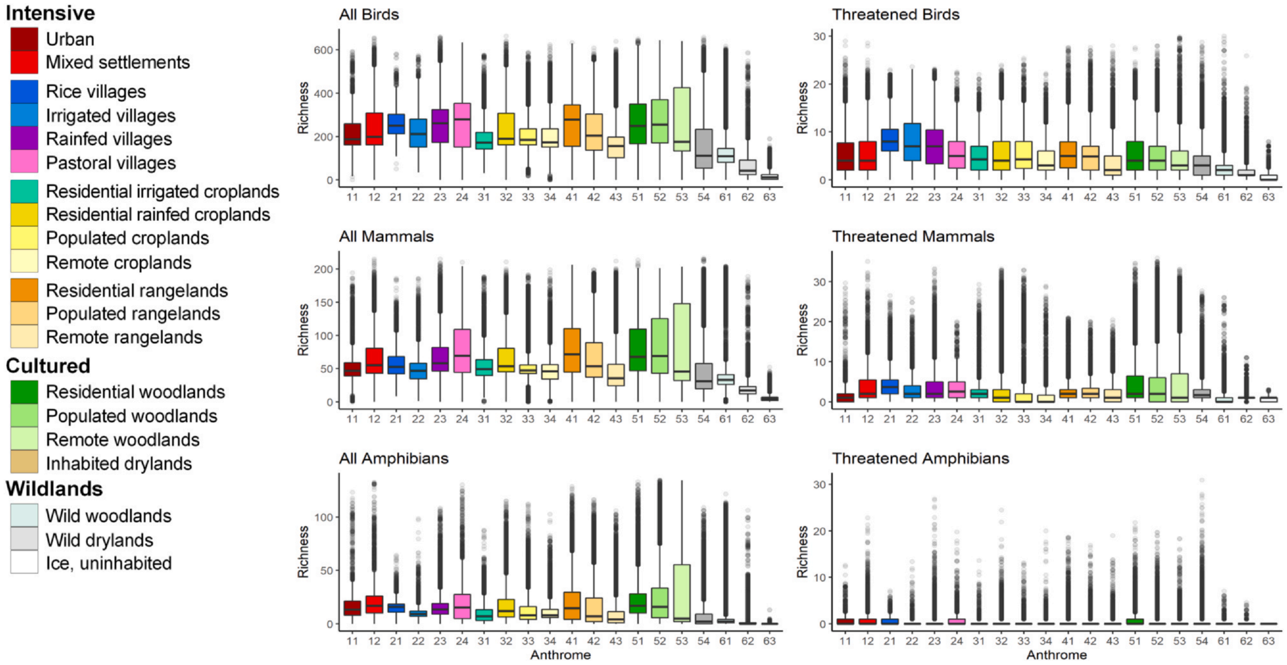

Fig. 1. Boxplot and outliers of richness of all and threatened birds, mammals, and amphibians across anthromes. Richness data from Jenkins et al. (2013) and Pimm et al. (2014). Anthromes from Gauthier et al. (2021).

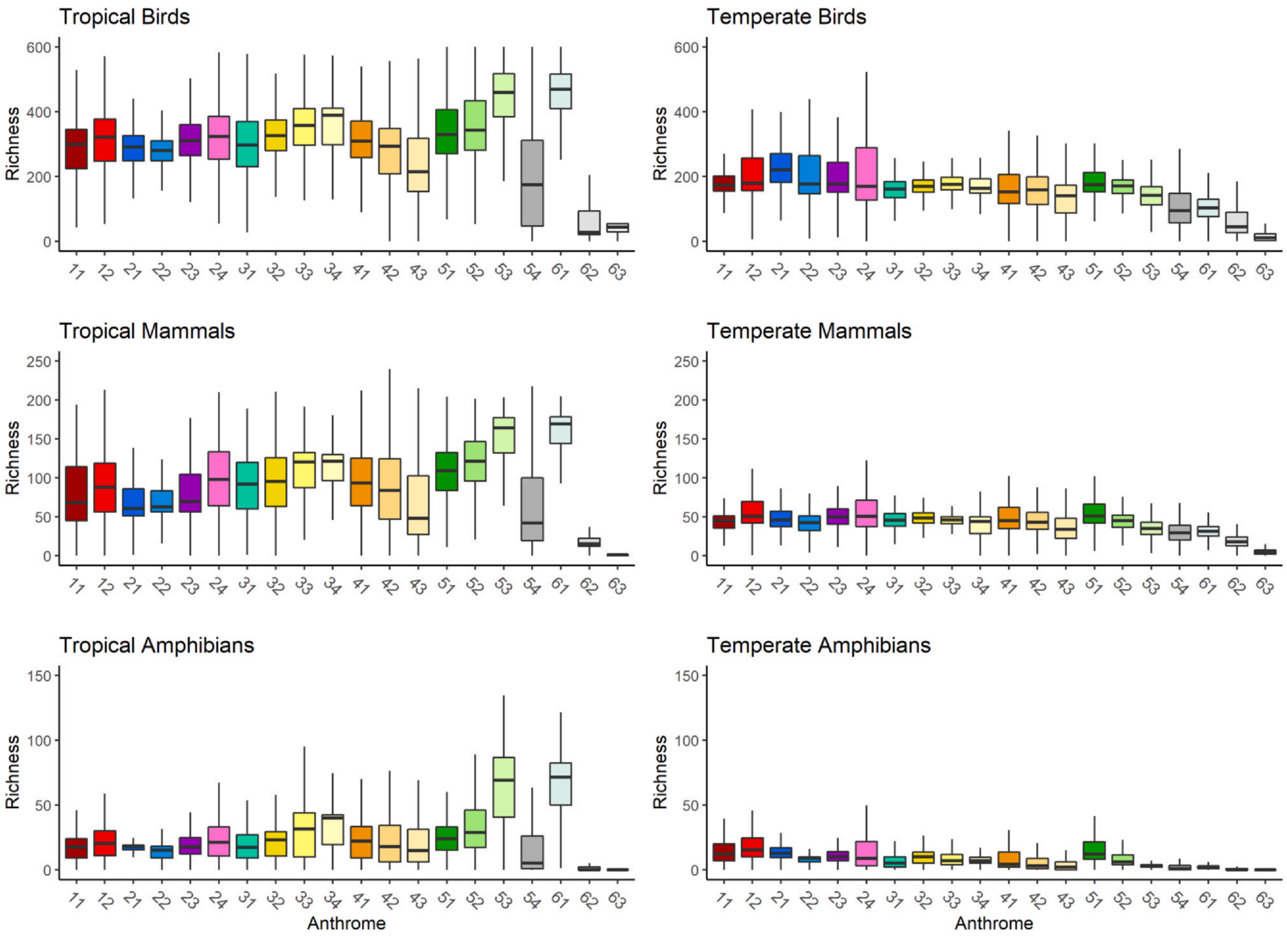

Fig. 2. Median richness of all birds, mammals, and amphibians by anthrome type in tropical and temperate regions. Richness data from Jenkins et al. (2013) and Pimm et al. (2014). Anthromes from Gauthier et al. (2021).

Table 2
Summary of median richness for all and threatened bird, mammal, and amphibian richness across temperate and tropical regions.

Anthrome		Bird				Mammal				Amphibian			
		Total		Threatened		Total		Threatened		Total		Threatened	
Class	Label	Trop	Temp	Trop	Temp	Trop	Temp	Trop	Temp	Trop	Temp	Trop	Temp
Dense Settlements													
11 Urban		301	173	8	3	68	45	4	1	18	12	0	0
12 Mixed settlements		322	179	6	4	87	50	4	1	20	15	0	0
Villages													
21 Rice villages		290	221	8	8	60	46	5	2	18	13	0	0
22 Irrigated villages		280	178	9	6	63	42	5	1	15	3	0	0
23 Rainfed villages		310	177	9	5	69	50	4	1	17	10	0	0
24 Pastoral villages		324	171	6	4	97	51	3	2	21	9	0	0
Cropland													
31 Residential irrigated croplands		297	161	7	4	92	46	4	1	17	5	0	0
32 Residential rainfed croplands		327	169	8	3	95	49	3	1	23	10	0	0
33 Populated croplands		359	176	11	4	120	46	6	0	32	7	0	0
34 Remote croplands		389	164	10	3	121	44	7	0	40	7	0	0
Rangeland													
41 Residential rangelands		309	152	6	3	94	45	2	2	22	4	0	0
42 Populated rangelands		294	159	5	4	84	43	2	2	18	3	0	0
43 Remote rangelands		215	140	3	2	48	34	2	1	15	2	0	0
Seminatural													
51 Residential woodlands		330	174	6	3	109	51	4	1	24	12	0	0
52 Populated woodlands		343	171	5	2	121	45	5	0	29	6	0	0
53 Remote woodlands		459	142	5	2	164	35	8	0	69	3	0	0
54 Inhahited treeless & barren lands		174	95	3	3	42	29	2	1	5	1	0	0
Wildlands													
61 Wild woodlands		469	103	5	2	169	31	8	0	72	2	0	0
62 Wild treeless & barren lands		28	45	1	1	15	18	1	1	0	0	0	0
63 Ice, uninhabited		44	11	2	0	1	4	0	1	0	0	0	0

richness in temperate regions was greatest in residential woodlands, mixed settlements, and villages. Amphibian richness ranked highest in dense settlements, rice villages, and residential woodlands.

3.2.2. Threatened species

Median threatened bird richness was greatest in cropland anthromes in tropical regions and villages in temperate regions (Fig. 3). Median threatened mammal richness was greatest in remote and wild woodlands in the tropics, though croplands were high in threatened species. In temperate regions, villages had the highest threatened median richness. Median richness of threatened amphibians was low across anthromes though there were outliers across all anthromes that reached 15 or more threatened species. Though most anthromes had few threatened species (< 10) there were outliers in many areas in each anthrome with 3x that number (Appendix Fig. 1b).

3.3. Geographic region

When subsetting the data by geographic region, heterogeneity of biodiversity within anthromes became clearer (Appendix Fig. 2a–f). There was higher richness of birds in dense settlements of Africa, Latin America, and Oceania, of mammals in residential and populated woodlands in Africa and Asia, and of amphibians across many regions in semi-natural anthromes. We also see low richness of threatened birds in Europe, many threatened mammals across anthromes in Asia, and many, though they are outliers, threatened amphibians in Latin America. From these data several clear opportunities and risks emerge. For example, what can region specific conservation efforts learn from the apparent success of bird conservation in Europe as evidenced by the low number of threatened birds? In Asia we see both high total and threatened mammals providing an example of spatial correlation between measures of richness.

3.4. Correlation between groups

At a global extent, there is a strong positive correlation ($r = 0.81$, p-value < 0.001) between the median richness of all and threatened bird species, a weaker correlation ($r = 0.480$, p-value $= 0.034$) between median richness of all and threatened mammal species, and no correlation between the median richness of all and threatened amphibian species ($r = 0.244$, p-value $= 0.314$). Between taxa, there was a positive correlation ($r > 0.5$, p-value < 0.05) suggesting opportunity for combined efforts for different vertebrates in anthromes. There was a negative, but nonsignificant (p-value > 0.10) between richness of all species in each taxonomic group and the ratio of non-threatened to all species across anthromes.

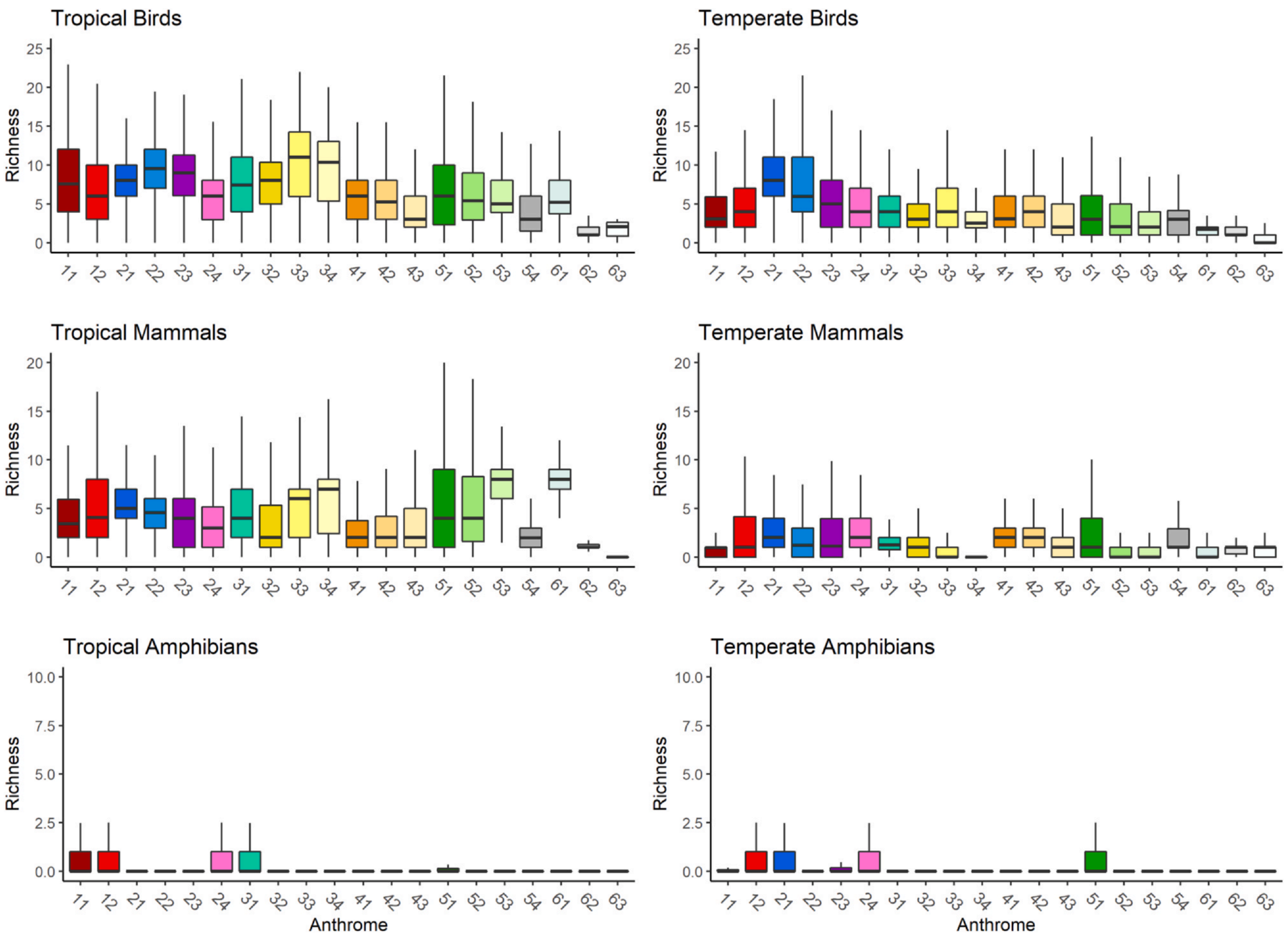

Fig. 3. Median threatened richness of birds, mammals, and amphibians by anthrome type in tropical and temperate regions. Richness data from Jenkins et al. (2013) and Pimm et al. (2014). Anthromes from Gauthier et al. (2021).

3.5. Response to Interventions at a global extent

Scaling back to the global extent, across anthromes, the best models (i.e., with the lowest AIC value) of median richness of all species included biodiversity hotspot. When significant (95% confidence intervals of the estimates not overlapping zero, Appendix Table 1), richness of all species increased as a function of percent biodiversity hotspot (Fig. 4a). Threatened avian richness across anthromes was lower when a greater proportion of that anthrome was protected (Fig. 4b). Thus, we may not be protecting landscapes in anthromes with the greatest number of threatened species. Threatened mammal richness was higher in anthromes when more of that anthrome was a hotspot (Fig. 4b).

4. Discussion

Anthropogenic, managed, and novel ecosystems, including cropland, rangeland, cities, and peri-urban landscapes, continue to expand in extent and impact (Ellis et al., 2021). Land for the production of food, fiber, and fuels encompasses at least 39% of Earth's ice-free surface (Foley et al., 2005) and while cities only cover approximately three percent of the world's surface area, their impacts extend far beyond municipal boundaries (e.g., Brown and Quinn, 2018). Thus, conservation prioritization schemes at local (e.g., Gibson and Quinn, 2017), regional (UK farmland birds; Vickery et al., 2004) and global (e.g., Half Earth; Mehrabi et al., 2018) scales should reflect the influence of humans on the landscapes we live, farm, and recreate in. However, there needs to be a balance between considerations of human pressure (e.g., O'Bryan et al., 2020) and recognition of conservation opportunities beyond protected areas (Martin et al., 2014). Thus, academic research and conservation practice needs to recognize and support investment in conservation opportunities in areas or anthromes that may have historically been neglected or negated because of a perceived lack of value due to human modification. The data presented here help prioritize opportunities (i.e., anthromes with high species richness) and challenges (i.e., anthromes with high threatened species richness) for three groups of vertebrate species. Additionally, linking patterns in anthromes with and across three taxonomic groups and with other essential biodiversity variables allows for a more focused and coordinated conservation effort.

4.1. Global and regional patterns

At a global extent, results show high variation within and between vertebrate species richness across anthromes and reveal insight into specific anthromes of importance for conservation prioritization. Vertebrate species richness is consistently low in barren and wildlands and higher in villages and rangelands, consistent with the Ellis et al. (2012) analysis of plant species richness. Pastoral villages, residential rangelands, and residential woodlands have among the highest total species richness for both birds and mammals. Pekin and Pijanowski (2012) showed that the probability of species endangerment in mammals increases with urbanization and high-intensity crop production at a global scale. Their analysis, using Anthromes V1, identified mosaic urban, village, and cropland anthromes as negative drivers of species richness. Our analyzes show that village anthromes, specifically rice and pastoral villages, exhibit high median richness for all species and for threatened species suggesting the importance of considering both threatened and all species richness and the relationship between the two measures of biodiversity. This matches well with Martin et al. (2014) who ranked village anthromes as the greatest opportunity for conservation based on spatial prioritization and protected area gap. An overlap of high richness across multiple taxa in village anthromes reveals the possibility of high-level conservation prioritization targeting multiple taxonomic classes; however, it is necessary to examine these patterns further at smaller spatial extents.

As a global dataset, anthromes allow for comparison of biodiversity patterns as a function of population density and land use intensity at different subunits. Consideration of richness in anthromes between temperate and tropical regions highlights the value of populated woodlands and croplands across taxa in tropical systems as compared to dense settlements and village anthromes across temperate regions, suggesting a pathway for further consideration of conservation efforts in these respective landscapes. Wild woodlands of the tropics also were higher in relative richness in tropical regions but not in temperate regions; thus, conservation prioritization efforts and discussions of tradeoffs should consider the climatic region when evaluating conservation priorities for managed ecosystems. For example, the conservation value of investment in land sharing versus land sparing may need to differ between tropical (e.g., Chandler et al., 2013) and temperate (e.g., Quinn et al., 2012) regions before making broad or conclusive statements. Similarly, we can consider patterns within biogeographic realms. For example, Brum et al. (2013) found that village anthromes have a negative influence on threatened amphibian richness in New World ecoregions. Although we did not observe the same pattern, we saw clear differences between tropical and temperate regions, indicating anthrome- and region-specific conservation opportunities.

4.2. Correlation between groups

Among birds and mammals at a global scale, we found a positive relationship between the distribution of all species richness and threatened species richness across anthromes. This presents an opportunity for conservation to keep common species common and highlights the importance of considering biodiversity variables beyond threatened species. We found no association between all and threatened amphibian richness, perhaps because of low levels of threatened richness of amphibians across anthromes.

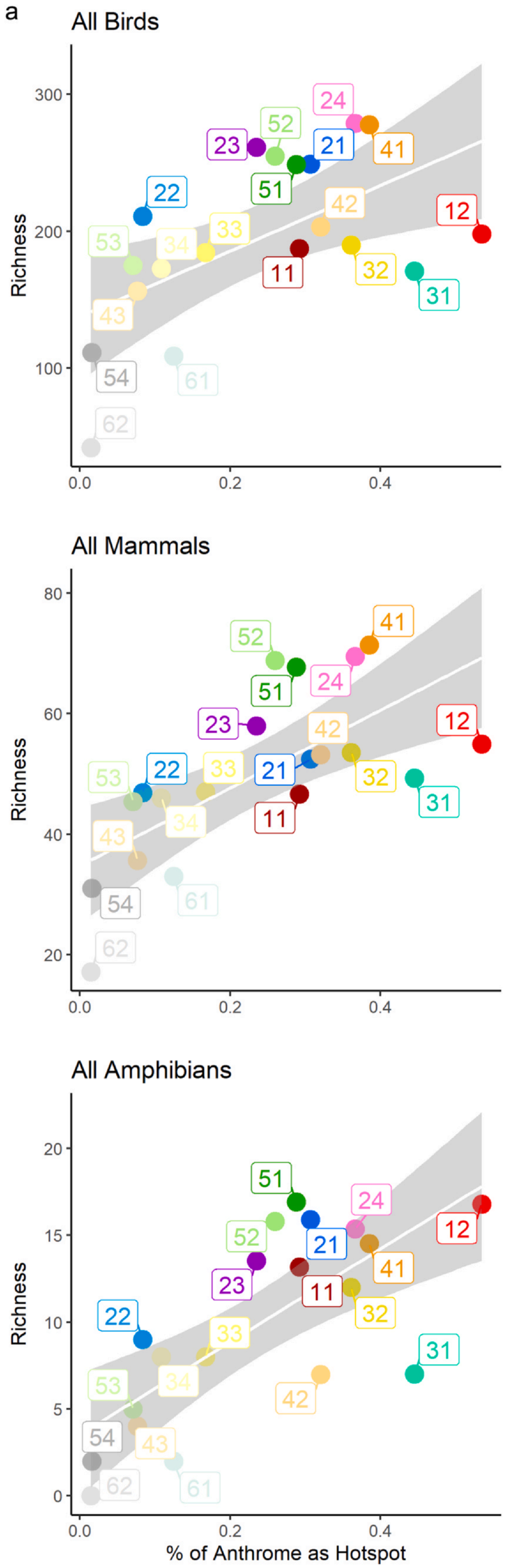

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Fig. 4. a. Median richness of all species as a function of percent biodiversity hotspot. Gray areas show the confidence interval around the regression line. Please refer to Fig. 1 for color-coding. b. Median threatened bird or mammal species richness as a function of percent protected or hotspot. Gray areas show the confidence interval around the regression line. Please refer to Fig. 1 for color-coding.

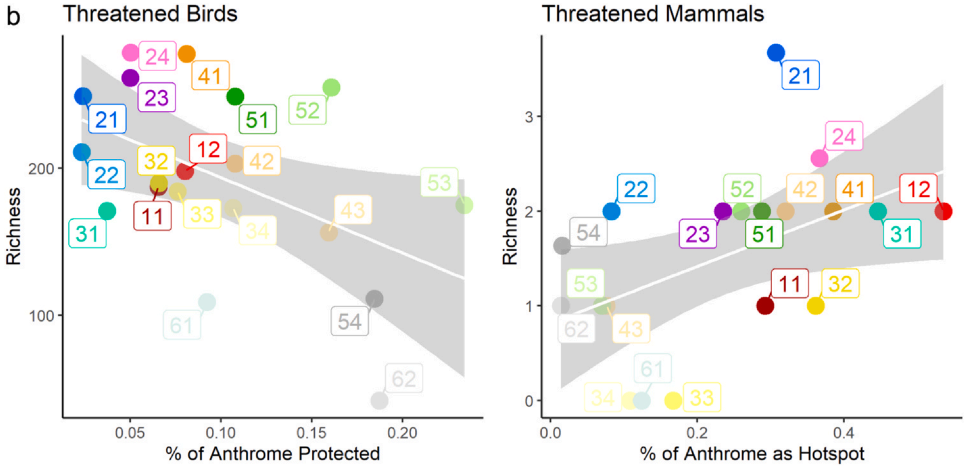

Fig. 4. (*continued*)

These positive correlations also highlight that consideration of the number of threatened species as a standalone essential biodiversity variable may obfuscate the reason for a high level of threatened species. For example, a high richness of threatened species in an anthrome may reflect the fact that there are more species present as much as the actual threat level to those species. We did find however, that when we considered the number of threatened species as a function of total species, there was no correlation. By linking richness and threat levels, hypotheses and questions can be proposed for further research. For example, if total richness is high and threatened species richness is low, does this imply good conservation management on the ground? Likewise, if both metrics are high, is it the result of bad management, a sampling artifact, or due to increased endemic species? Future research could link governance practices to these analyzes, building on consideration of relationships with protected areas discussed below.

4.3. Response to interventions at a global extent

We tested how protected areas and hotspots aligned with anthromes of highest priority (either all species richness or threatened species richness) as an indicator of alignment between need and action. We found that for two vertebrate taxa (mammals and amphibians) there was not a relationship between protected area and richness suggesting that our protection efforts are not aligned with conservation needs, concurring with past research suggesting that the placement and overlap with conservation priorities are not meeting global targets (Venter et al., 2014; Watson et al., 2014). Furthermore, there was a negative relationship between threatened bird richness and protected area suggesting an over-allocation of resources in some regions based on bird richness. The relationship between hotspot and richness is intuitive given the definition of a hotspot (high endemism + high population density). However, it is suggestive that anthromes could be used to extend the hotspot model of conservation into a global gradient of opportunity and threat. Thus, anthromes can serve as a quantitative measure that extends the narrative of prioritization in hotspots to a global extent as compared to an either/or classification as currently applied.

The multiple extents of our analyzes represent broad spatial scales and thus our results may vary in their ability to inform local conservation action. However, we believe our results can help shape global and regional prioritization efforts across multiple taxa. Future research should consider individual species of conservation need or other essential biodiversity variables. Likewise, it would be valuable to test competing models of specific landscape factors within anthromes that affect vertebrate richness; for example, irrigation or tree cover.

In conclusion, this first comprehensive analysis of current terrestrial vertebrate richness by anthrome builds on important work focused on richness biomes, ecoregions, and political units (Hoekstra et al., 2005; Chape et al., 2005; Allan et al., 2018). We have extended these global scoping efforts to include anthromes incorporating measures of human population size and land use intensity. Subsets of the data at different spatial extents highlight regional variation, but the global message is clear: species richness is consistently high or highest in anthromes that include people. These data are valuable for global conservation organizations as an updated framework that can be used to prioritize global resource allocation while considering both natural and human systems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01591.

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