Biological Conservation 279 (2023) 109944

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Are we hunting bats to extinction? Worldwide patterns of hunting risk in bats are driven by species ecology and regional economics

Krizler Cejuela Tanalgo[a,b,c,*], Tuanjit Sritongchuay[d], Angelo Rellama Agduma[b,e,f], Kier Celestial Dela Cruz[b], Alice C. Hughes[g,**]

[a] Landscape Ecology Group, Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun 666303, China
[b] Ecology and Conservation Research Laboratory (Eco/Con Lab), Department of Biological Sciences, College of Science and Mathematics, University of Southern Mindanao, Kabacan 9407, Cotabato, Philippines
[c] Zukunftskolleg and the Centre for Advanced Study of Collective Behaviour, University of Konstanz, Universitätsstrasse 10, Baden-Württemberg, Konstanz 78457, Germany
[d] Helmholtz-Centre for Environmental Research-UFZ, Department of Computational Landscape Ecology, Leipzig 04318, Germany
[e] State Key Laboratory for Conservation and Utilization of Subtropical Agrobioresources, Guangxi University, Nanning 530004, Guangxi, China
[f] Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning 530004, Guangxi, China
[g] School of Biological Sciences, The University of Hong Kong, Hong Kong 999077, China

ARTICLE INFO

Keywords:
Anthropogenic threats
Covid-19
Redlist
Tropics
Wildmeat

ABSTRACT

Bats are routinely neglected in conservation, often regarded as uncharismatic and constantly maligned despite their provision of economic and ecosystem services. Yet many species are threatened, and while the loss of roosting and foraging habitat has been explored, the impacts of hunting on species survival are less well understood. Here, we analysed the hunting risk of 1320 bat species (of 1400 known) from around the world and explored the association between ecological traits and socioeconomic variables. Globally, at least 19 % of species are threatened by hunting. Large-bodied bats with narrow distributions are at increased risk of hunting, particularly in tropical regions. Multiple threats, such as habitat loss and modification, are likely to exacerbate the pressures experienced by hunted species. Furthermore, accessibility to bat habitats and low-income drive bat hunting in developing countries. With the global economic recession and the need for economic recovery following the pandemic, hunters may rely more on wildlife for subsistence and pose a threat to both biodiversity and public health. Achieving the balance between economics and conserving biodiversity is challenging due to socioeconomic factors, and the complex interplay of different forms of threat. Therefore, interventions to reduce bat hunting activities should include greater investment to facilitate sustainable livelihood development in the rural economy, and elevating public knowledge about bat ecosystem services, and their potential role in the transmission of zoonotic diseases.

1. Introduction

Humans depend on key ecosystem services to ensure access to resources needed for stable life quality. However, prioritizing short-term economic gain over long-term environmental implications poses an ever greater threat to ecological stability (Caro et al., 2012; Corlett, 2015), including the provision of key ecosystem services (Ceballos et al., 2015). It is estimated that at least 900 species of vertebrates have gone extinct in the last 500 years, and another 3500 are threatened, with at least one in four mammals facing a high risk of extinction (IUCN Red List, 2021; Ritchie and Roser, 2021). However, reducing this threat and better conserving species is challenging, and further efforts are needed, particularly for species that are often perceived as less 'charismatic' (Arponen, 2012; Brum et al., 2017; Cerri et al., 2022). The potential for even common and abundant species to become threatened or even extinct as a consequence of high levels of pressure from activities such as hunting is known as the 'Passenger-Pigeon fiasco', which is especially important given that many species perceived as common lack

* Correspondence to: K. C. Tanalgo, Ecology and Conservation Research Laboratory (Eco/Con Lab), Department of Biological Sciences, College of Science and Mathematics, University of Southern Mindanao, Kabacan 9407, Cotabato, Philippines.
** Corresponding author.
E-mail addresses: tkrizler@gmail.com (K.C. Tanalgo), ach_conservation2@hotmail.com (A.C. Hughes).

https://doi.org/10.1016/j.biocon.2023.109944
Received 12 November 2022; Received in revised form 28 December 2022; Accepted 30 January 2023
Available online 9 February 2023

overarching legislative measures for protection (Rainforest Rescue, undated; Tanalgo and Hughes, 2019, 2018).

Despite the important ecosystem services they provide, such as pollination, seed dispersal, and pest consumption, bats generally receive less conservation attention than species perceived as large and charismatic (Frick et al., 2020; Macdonald et al., 2015; Tanalgo et al., 2022). In addition to the loss and degradation of habitats, hunting is a major direct threat to many species (Fritz et al., 2009a, 2009b; Jones et al., 2003). Bat hunting is widespread, particularly for large-bodied and colony-roosting species, which are easy targets for hunting (e.g., harvesting colonies of cave-dwelling bats or shooting tree-roosting bats) (Sagot and Chaverri, 2015; Tanalgo et al., 2022). Bats are particularly vulnerable to the impacts of hunting due to their low reproductive rate and high age of maturity, hindering their ability to recover from

Table 1
Summary of traits used to predict hunting risk and their potential impacts on population.

Predictors	Scope	Hunting exposure	Potential impacts on the population
Biotic variables			
1. Body mass	Average to maximum body mass of an adult bat.	Hunters prefer larger species, as larger bats are more visible, provide a bigger reward and are easier to find.	Large-bodied and herbivorous species have higher extinction rates because of their slower reproductive rate, smaller population size on average, and vulnerability to extirpation because of roosting habits.
2. Trophic level	Position of the species in the food chain.	Herbivorous bats are more vulnerable to hunting because they have larger body sizes on average and often aggregate in large numbers.	
3. Roosting habitat breadth	Number of roosting habitats occupied by bats.	Populations that roost in limited habitat types are predictable and more prone to hunting.	Habitat specialist species will have less capability to move to another habitat when hunting events and other threats occur, thus increasing their extinction risk.
4. Sociality	Species cluster within its habitat.	Colonial bat species such as cave-dwelling bats and some species of flying foxes which roost in aggregations are more visible in their roosting colonies and are easier to locate and hunt.	Clustered populations are easily extirpated during hunting events and will have slow population recovery.
Geographical variables			
5. Distribution range	Geographical area within which bat species occur.	Species with limited ranges are more vulnerable to hunting because of their limited ability to disperse during hunting events and are likely to form small populations.	Species with narrower ranges tend to have limited niche distribution and are more vulnerable to hunting and other threats within their range, thus increasing their extinction risk.
6. Geopolitical endemism	Species occurrence within a country or geopolitical boundary.	Island and geopolitically endemic species are likely to be hunted because they may represent a major protein source on a single territory or islands and may be vulnerable due to small ranges.	
7. Island endemism	Species occurrence within an island.		
Conservation status variables			
8. Threatened status (threatened)	Binomial conservation status of bats according to the IUCN redlist category.	Threatened species tend to have narrower distribution ranges.	Hunted species that are already in the threatened category have higher extinction probabilities.
9. Number of threats	Number of threats per bat species.	Species exposed to other threats tend to be more exposed to hunting (e.g., hunting occurs after extreme weather events).	Other threats may decrease the capacity of the population to recover from hunting events.
Habitat protection variables			
10. Forest cover	Estimated forest cover per country.	Reduced forest cover increases species detectability and access; and limits species distribution across its habitat due to limited areas for roosting. Higher forest cover indicates better environmental protection with a lower number of threatened species in a country.	Forest-dependent species may increase their extinction risk.
11. Protected area	Percentage of the country area with protected area zone.	Higher percentage of protected areas reduce the vulnerability of species to hunting. A higher percentage of protected areas means more species are protected from exploitation and human conflicts.	Species outside protected areas (i.e., without statutory protection) will increase extinction risk from hunting due to higher exposure, accessibility, and lower quality of habitat for population recovery.
Human pressure variables			
12. Total population	Number of people in a country at a given time.	Higher human population increases human-bat conflict and exploitation of natural resources, including the hunting of a higher number of threatened species.	Increasing population may increase demands for wild meat, particularly in rural areas where people tend to rely on wild meat.
13. Gross National Income (GNI)	Total amount of money that people and businesses can earn in a country. Indicator of national development.	Lower GNI increases the human necessity to exploit wildlife species for subsistence.	Countries with lower GNI will have a lower capacity to protect their species or implement recovery plans.
14. Livestock Production Index (LPI)	Livestock production index is the output index of animal livestock products, including meat, milk, eggs, etc. in a country.	Higher LPI indicates a higher reliance of people on livestock or meat products. With a decrease in livestock production, people may shift to hunting of accessible wild meat such as bats. Increasing livestock production increases the potential interaction between bats and livestock.	
15. Number of species hunted	Estimated total number of species hunted in a country.	A higher number of hunted species increases the probability of reducing the bat population and the increasing the number of threatened species in a country.	Increased number of species hunted increases the extinction rate within a country.

population loss (Jones et al., 2003). Understanding hunting is complex and often involves different socioeconomic and cultural motivations, but food subsistence in rural areas is a major factor (Mildenstein et al., 2016; Oedin et al., 2021). National policies to protect or regulate bat hunting are either absent or lack enforcement in many countries, and sometimes bats are considered vermin (Medellin et al., 2017; Oedin et al., 2021). For example, the Mauritian government culled at least 50,000 endangered and endemic Mauritian flying foxes (*Pteropus niger*), representing approximately 40 % of the population on the islands of Mauritius and La Reunion, to reduce their population, as farmers claimed that they damaged orchards (Florens, 2016a). Furthermore, common and hyperabundant species can be particularly vulnerable to hunting due to their large populations and lack of protection, such as the frugivorous *Rousettus amplexicaudatus* in the Philippines (Tanalgo and Hughes, 2019). At least 37 % (201 species) of Old World fruit bats play a crucial role in ecosystems, such as pollination and seed dispersal for thousands of plant species (Aziz et al., 2021). Yet, continuous hunting results in defaunation, or reduced populations, which negatively affects key ecological processes provided by bats. For example, the reduction of frugivores may drive changes in vegetation structures, especially through the loss of seed dispersers (Bello et al., 2015; Stoner et al., 2007). Therefore, unsustainable hunting has irrefutable consequences for natural ecosystems. However, most studies on wildlife hunting and harvesting analyses are biased towards large and threatened species. For example, Ripple et al. (2016) examined the hunting risks of global mammals, but their data may have overlooked a large proportion of bats as they only included 27 species (3 %), which is a tiny percentage of the species known to be hunted (167 species from Mildenstein et al., 2016). Consequently, such an analysis cannot gauge the potential threat of hunting on species that were excluded from the analysis.

Mapping threat is essential to develop better conservation interventions (Hughes, 2017; Tanalgo et al., 2022; Tulloch et al., 2015). Except for existing predictive spatial modelling to determine hotspots where wildlife hunting can potentially occur or impact wildlife populations (Harfoot et al., 2021), there are limited measures of hunting pressures at the country level for any taxonomic group, particularly for bats. In this analysis, our objective was to understand the patterns and determine the drivers of bat hunting on a global and regional scale. Based on previous hunting analysis for other mammalian taxa, we hypothesised that larger species (e.g., Pteropodid bats), especially those with limited range in the tropics are more vulnerable to hunting (Atwood et al., 2020; Price and Gittleman, 2007; Welch and Beaulieu, 2018). Consequently, we expected that overall species will be most vulnerable to extinction as a consequence of hunting in the Old World, although risk of being hunted will be present across much of the tropics, and will also relate to the accessibility of roosts, and the size and predictability of roost sites. Obviously, threat from hunting will not occur in isolation, and thus we expect species with smaller ranges, and those limited to islands may be most vulnerable to potential extinction as a consequence of hunting. To test this, we selected fifteen variables representing various facets of species ecology, endemism, threats, and country socioeconomic status (summarised in Table 1) which may indicate species risk from hunting, either in terms of exposure to hunting or threat from hunting. First, we collated the list of bat species hunted and mapped their distribution worldwide. Second, we assessed and compared threats experienced by hunted species. Lastly, we investigated the relationship between ecological and socioeconomic variables and the risk of species being hunted and discuss how species might be better protected. We aim to assess the extent of hunting as a threat to bats and inform better policy and management and highlight the need for more balanced funding based on potential vulnerability.

2. Materials and methods

2.1. Species database

The species hunting risk was analysed in different levels based on species ecology, threatening process, and national socioeconomic status (Fig. 1). We built and standardised our dataset for 1329 bat species listed in the latest IUCN Red List database (version 2022-1) and curated species names according to Simmons and Cirranello (2020). Species categorised as extinct or extinct in the wild were excluded from the analysis. Species were then categorised according to redlist threat status and levels of endemism (geopolitical endemism and island endemism) (see Tanalgo et al. (2022) for comparative species diversity analysis). We standardised our bat hunting assessment by filtering the IUCN redlist database (version 2022-1) database of 'threat' and 'trade and use' for all bat species to assess the species as 'hunted'. All species known to be harvested for subsistence, medicine, game, trade, and other forms of direct human use were classified as hunted species. To avoid potential biases, since the IUCN redlist database may be incomplete, or not up-to-date to indicate accurate known threats to species (Harfoot et al., 2021; Hayward, 2009; Trull et al., 2018), we cross-referenced synthesis papers on bat hunting and harvesting to improve our assessment (e.g., Mickleburgh et al., 2009; Mildenstein et al., 2016; O'Shea et al., 2016).

The database also included other biological and ecological factors such as geographic range and species traits (adult body mass (g) (Faurby et al., 2018), trophic levels (e.g., herbivores, predators, and omnivores) following the classifications by Atwood et al. (2020), evolutionary distinctiveness (ED) (Isaac et al., 2007), roosting habitat and roosting strategy). For roosting habitat, we assigned a simplified roosting preference for each species following Sagot and Chaverri (2015): (i) cave-dwelling (caves and crevices), (ii) tree-dwelling (tree cavities, tree bark, and tree boles), (iii) foliage-dwelling (leaves and modified leaves and stems, and foliage and plant structure), and (iv) human-made (buildings and houses). Furthermore, sociality was classified according to roost aggregations (e.g., solitary or colonial) based on observed species natural history accounts. Solitary species roost singly or in pairs and do not form large aggregations. Whereas colonial species are populations that form large colonies or aggregations that surpass a single-family group. We used all these variables as predictors of the risk of species hunting.

2.2. Evolutionary distinctiveness and threat index

We assessed and compared the evolutionary distinctiveness (ED) of hunted and non-hunted species and considered geopolitical endemism using the dataset from Isaac et al. (2007). Evolutionary distinctiveness (ED) is the degree of species uniqueness within the taxonomic evolutionary tree. We quantified threats to hunted and non-hunted species using the IUCN redlist data, and classified them following the simple threat classification contextualised for bats and their habitats (Tanalgo et al., 2022). We then calculated the Species Threat Index (STI) (Tanalgo et al., 2022) based on the calculated quotient of the sum of the number of threats ($T_{\text{dir, ind, nat}}$) and the number of threats ($N^o\ T$) (STI species = $\Sigma\ T/N^o\ T$). We then compared STI between hunted and non-hunted species within each category of geopolitical endemism.

2.3. Extinction and hunting risks

The species extinction risks of hunted and non-hunted species were estimated across taxonomic groups, ecological status, and distribution, following Hoffmann et al. (2010) and Richman et al. (2015). The risk of extinction was calculated using the equation: $\hat{p}_{\text{extinction}} = N^o\ TH/(N^o\ SP - N^o\ DD)$, where $N^o\ SP$ is the total richness or number of species within the group, and $N^o\ TH$ is the number of threatened species based on the richness of species classified as 'Vulnerable', 'Endangered' and 'Critically endangered', and the number of Data Deficient species ($N^o\ DD$),

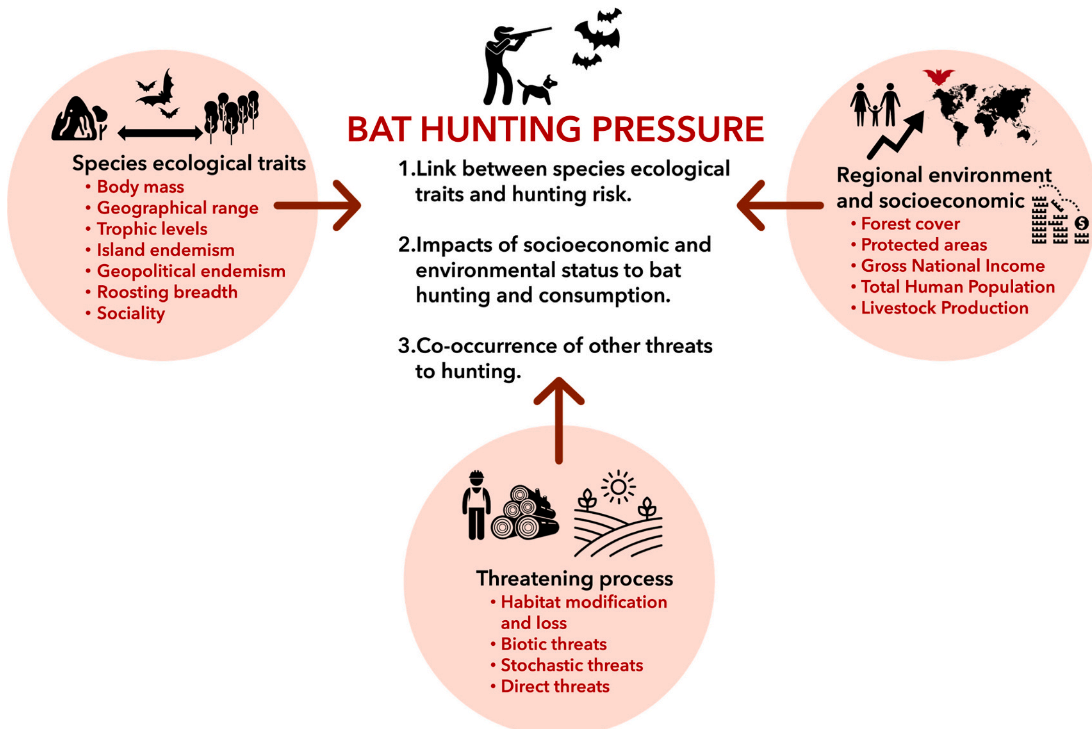

Fig. 1. Schematic diagram showing the analysis framework to assess link between species hunting risk to species ecology, threatening process, and national socioeconomic factors.

assuming that data deficient species will have a relatively similar risk of extinction as those species in threatened categories (Bland et al., 2015; Tanalgo et al., 2018; Welch and Beaulieu, 2018). The lower estimate of the extinction risk was then calculated ($\hat{p}_{\text{extinction\_lower}} = N^o\ TH/N^o\ SP$) if that *DD* species were not threatened and the upper estimates ($\hat{p}_{\text{extinction\_upper}} = N^o\ TH + DD/N^o\ SP$) assuming that DD is threatened.

We then predicted the drivers of hunting risk (hunted versus non-hunted) based on species biological and ecological traits using a binomial generalised linear model (GLM) with logit-link function. We built a model that included all explanatory variables that may be associated with bat hunting risk. Biotic variables included body mass, trophic level, roosting habitat breadth, and sociality. In addition, we included geographical variables including range, island endemism, and geopolitical endemism (Tables 1 and 2). Furthermore, we considered IUCN redlist threat status (e.g., threatened status and number of threats including habitat loss and modification, direct anthropogenic threats, and stochastic threats) as the predicting variables for our model. We assigned binary categories for species threat category following Atwood et al. (2020). Species classified as critically endangered, endangered, and vulnerable as 'threatened,' while species classified as least concerned and near threatened as 'non-threatened'. Species classified as Data Deficient were included as 'threatened' with the assumption that species listed as Data Deficient are more threatened with extinction (Bland et al., 2015; Tanalgo et al., 2022). Prior to modelling, we tested all continuous variables for autocorrelation and found none of the variables are autocorrelated ($r > 0.75$).

Table 2
List of binomial GLM candidates showing the relationship of biotic, geographic, and conservation status variables to predict hunting risk. Nine (9) predictor variables were included: mass (MAS), trophic groups (TRO), roost specialisation (SPE), sociality (SOC), geographical range (RAN), geopolitical endemism (GEO), island endemism (ISL), threatened status (THS), and number of threats (NOT). The best model was shown in bold.

Model	Terms	AIC_c	dAICc	$wAIC_c$
1	**MAS + TRO + SPE + SOC + RAN + GEO + ISL + THS + NOT**	**722.733**	**0**	**0.658**
2	MAS + TRO + SPE + SOC + THS + NOT	732.250	9.517	0.006
3	MAS + TRO + SPE + SOC + RAN + GEO + ISL	757.685	34.952	<0.001
4	MAS + TRO + SPE + SOC	912.672	189.939	<0.001
5	RAN + GEO + ISL	1054.611	331.878	<0.001
6	THS + NOT	1197.481	474.748	<0.001
7	MAS + RAN	843.071	120.338	<0.001
8	RAN	1132.746	410.013	<0.001

2.4. Hunting risk and regional socioeconomic factors

We created a country-based checklist for species vulnerability and hunting risk based on the country occurrence range using the IUCN country range map to compute the richness of hunted species per country. Here, we scored each country based on the occurrence of hunted bat species with the assumption that bat species are equally at risk of being hunted throughout their range, as while this may vary, obtaining an accurate representation of this across space and time is likely impossible (see for example Brierley et al., 2016). Using the same approach, we then quantified the richness of geopolitically endemic and threatened species per country. The estimated richness of bat species per country is a conservative estimate of the bats hunted worldwide. The analysis was carried out at the country level to avoid issues with species range maps, which have been found in the previous analysis. We extracted from the World Bank database (2022) the following national-level habitat protection variables (e.g., %protected area and %forest cover) and human pressure variables (e.g., total human population, Gross National Income, and Livestock Production Index) as our predicting variables of the number of hunted and threatened species at the country level. The GNI is a useful and accessible indicator that can be an effective economic proxy to indicate economic performance and other non-monetary measures of country living standards (International Monetary Fund, 2009) and has been used indicator in previous extinction and hunting risk analysis (Price and Gittleman, 2007). While we used the livestock production index as an indicator of dependence on livestock outcome, this index calculates the national livestock production output of husbandry meat and dairy products (World Bank database, 2022).

2.5. Data analysis

We log-transformed ($\log_{10}$ (x) or $\log_{10}$ (x) + 1) all our continuous data when necessary to improve the data distribution prior to analysis. The relationship between hunted and non-hunted species between taxonomic groups, trophic levels, and ecological variables was tested using the Chi-square test of association (χ^2). A nonparametric Kruskal-Wallis test or the Mann-Whitney *U* test was used to compare ED and STI. A similar test was used to determine the difference in the richness of hunted, endemic, and threatened species in biogeographical realms, and then the Spearman rank correlation test was used to determine their relationship. We then performed a global analysis to determine the relationship between hunting and extinction risks with socioeconomic variables. We used the complete GLM with Poisson distribution (logit link) to determine the effects of country forest cover (%), protected area (%), total human population, Gross National Income (GNI, USD), and Livestock Production Index (LPI, 2014–2016 = 100) (The World Bank, 2022) on the richness of hunted and threatened species. We considered eight (8) models for the hunting risk model (Binomial) and included all socioeconomic models for regional hunting rate (Poisson) (Table 2). We used the lowest Akaike information criterion (AICc) and Akaike weights (wAICc) in the selection of the most parsimonious model.

We performed all our statistical analysis and visualisation in open software JAMOVI version 2.2.2 (The Jamovi Project, 2020) and GraphPad Prism 8 (GraphPad Software, La Jolla California USA, 2021). All graphic silhouettes used were downloaded from Logomakr (https://logomakr.com/).

3. Results

3.1. Diversity and ecological status of hunted bats

Of the 1320 bats on the IUCN redlist, 19 % (N = 254 spp.) of them are hunted (Fig. 2). The highest proportions of species hunted by realm are in the Australasian (40 %, $N = 102$ spp.), Indomalayan (24 %, $N = 79$ spp.), and Afrotropical (22 %, $N = 62$ spp.) realms. In terms of taxonomic groups, most hunted species are larger-bodied superfamilies of Pteropodoidea (73 %, $N = 140$ spp.), as well as small bats within Rhinolophoidea (26 %, 52 spp.) ($\chi^2 = 450.113$, d.f. = 4, $P < 0.001$). Between trophic levels, hunting is significantly higher among herbivores (63 %, N = 140 spp.) than among predators (12 %, $N = 108$) and omnivores (3 %, $N = 6$ spp.) ($\chi^2 = 333.729$, d.f. = 2, $P < 0.001$). Threatened (24 %, $N = 107$ spp.; $\chi^2 = 8.333$, d.f. = 1, $P = 0.004$) and narrowly distributed species are more prone to hunting; for example, there are more geopolitically endemic species (25 %, $N = 74$ spp.) that are significantly more vulnerable to hunting than non-endemic species (18 %, N = 108 spp.) ($\chi^2 = 109.237$, d.f. = 1, $P < 0.001$) (Fig. 2).

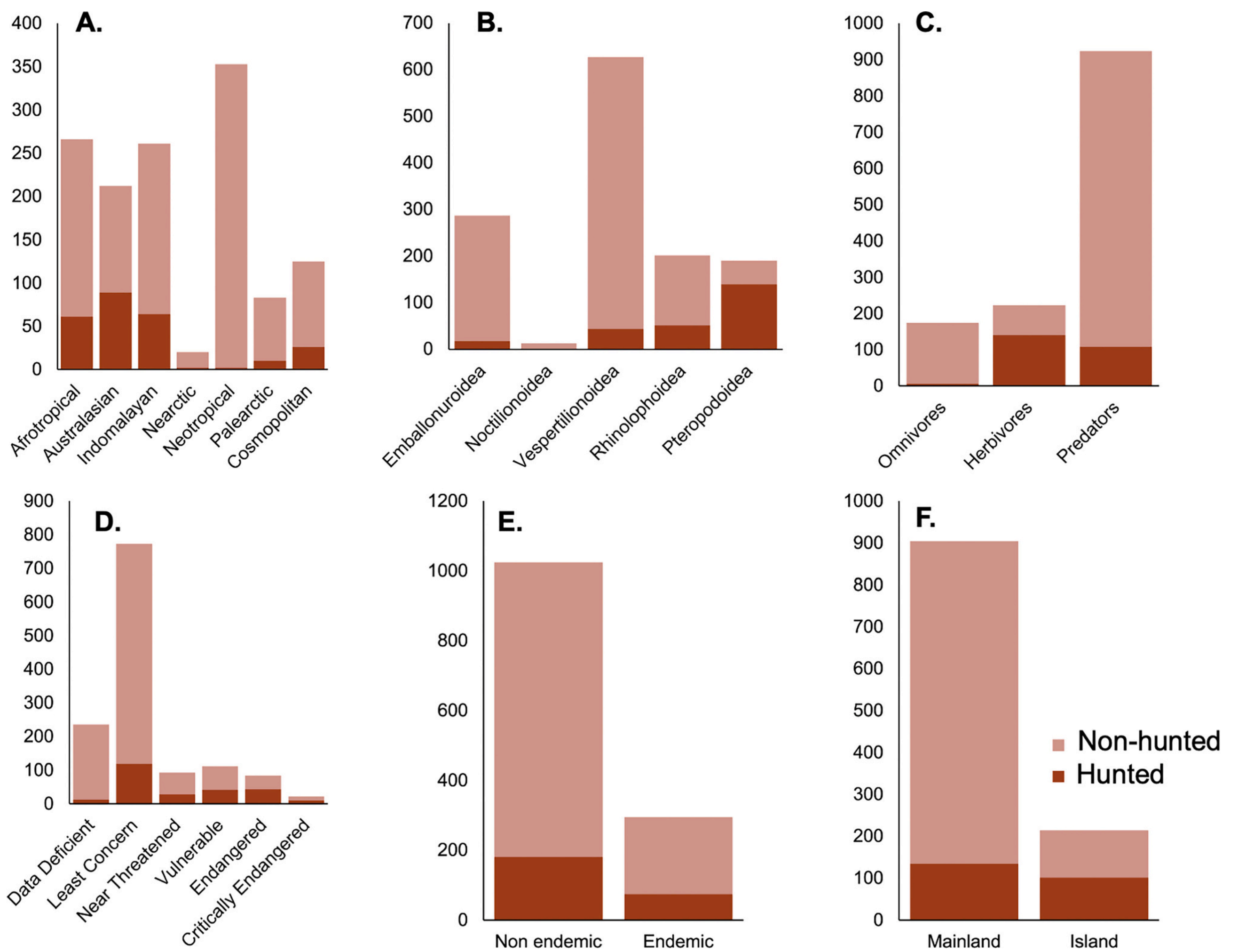

Fig. 2. Distribution and richness of bat species hunted worldwide according to endemism, conservation status, and other ecological variables (A. by region, B. by superfamily, C. by trophic groups, D. Conservation status, E. by geopolitical endemism, and F. Island endemism).

Furthermore, island species (47 %, $N = 101$ spp.) are at increased risk of being hunted compared to more widespread species in continental areas (15 %, $N = 134$ spp.) ($\chi^2 = 109.24$, d.f. $= 1$, $P < 0.001$). Threatened species (24 %, $N = 107$ spp.) are significantly more prone to hunting than those in non-threatened categories (17 %, $N = 147$ spp.) ($\chi^2 = 8.333$, d.f. $= 1$, $P = 0.004$). Hunting pressure was compared with the total number of species hunted according to roosting habitat. It showed that significant risk is only in the cave- and foliage-dwelling species. The highest hunting rate occurs in foliage-dwelling species (26 %, $N = 82$ spp.) followed by cave-dwelling species (24 %, $N = 132$ spp.). Although colonial species are significantly more hunted than solitary species.

3.2. Species evolutionary distinctiveness and threats

The evolutionary distinctiveness (ED) of the species differed significantly between hunted and non-hunted species (MWU test = 86,519, df = 1, $P = 0.010$) and endemism (KW test: $\chi^2 = 11.58$, d.f. $= 3$, $P < 0.010$) (Fig. 3A). Patterns of threats between hunted and non-hunted species varied depending on the type of threatening process. Apart from hunting and harvesting, 47 % of the hunted species also face deforestation as a major driver of population decline, followed by unregulated tourism (likely caving, or temple visits) (33 %) (Fig. 3B and C), while stochastic threats are poorly known for both hunted and non-hunted species (Fig. 3C). The threat index for hunted species is twice that of non-hunted

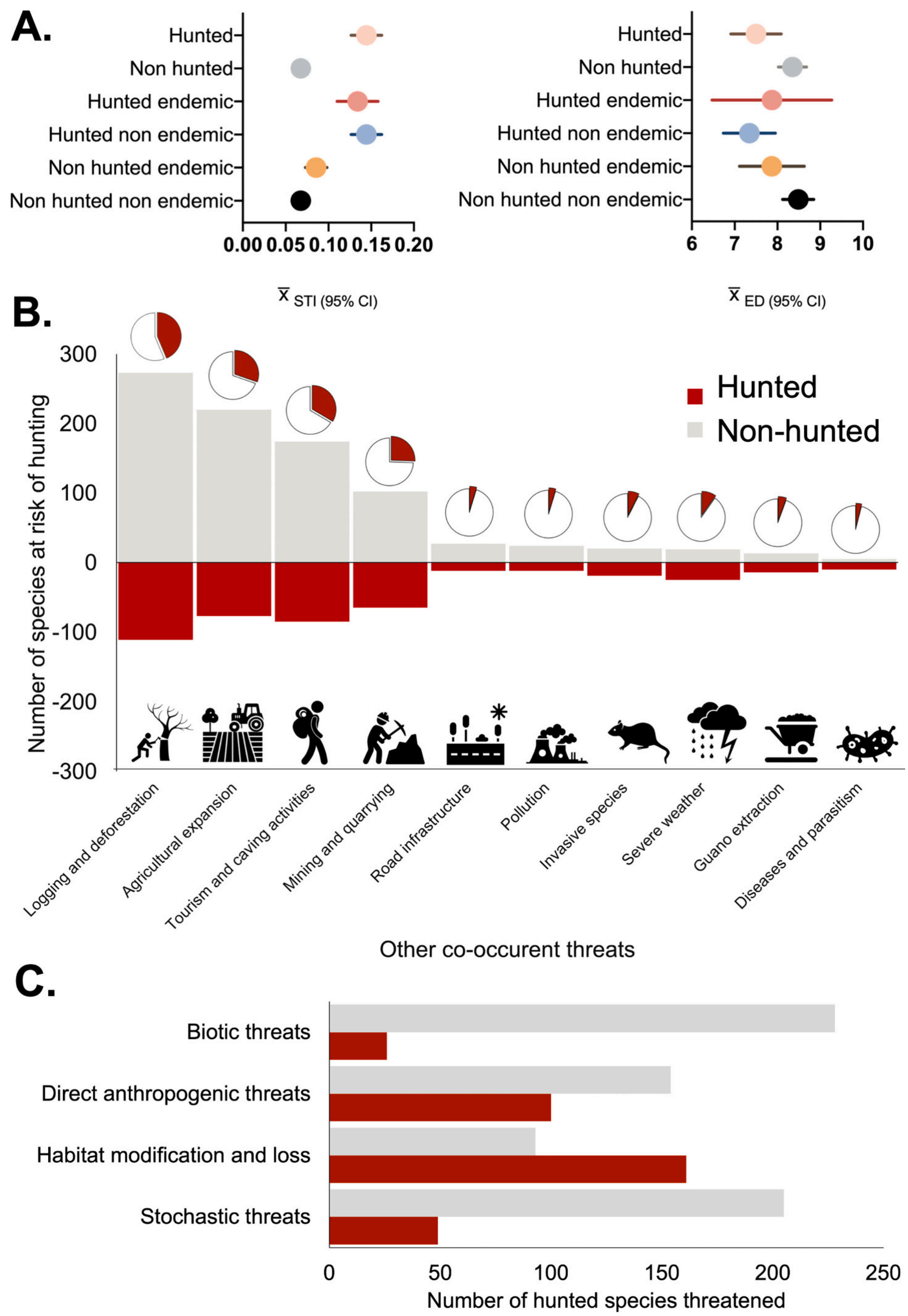

Fig. 3. Comparison of species evolutionary distinctiveness and threat index in hunted and non-hunted species between geopolitical endemism (A). Proportion (overall species threatened) of other threats to hunted and non-hunted species. The pie graph represents the proportion of hunted species compared to the overall number ($N = 254$ spp.) of species at risk of hunting. Comparison of hunted species across major threat categories (C).

species (MWU test = 46,664, df = 1, $P < 0.0001$). Furthermore, the threat levels of the hunted and non-hunted species differed when compared between the levels of geopolitical endemism levels (KW: $\chi^2 =$ 96.32, d.f. = 3, $P < 0.0001$) (Fig. 3A). We did not find a significant correlation between ED and STI in general and between hunted and non-hunted species (Spearman's $\rho = -0.031$, $P = 0.319$).

3.3. Extinction and hunting risks

We estimated and compared the extinction risk of hunted and non-hunted bats globally using the IUCN database. Extinction risk varied between measures of endemism and ecological traits, but hunted species are at higher risk of extinction (Global: $\hat{p}_{\text{extinction}} = 39$ %, 38–40 %) than non-hunted species (Global: $\hat{p}_{\text{extinction}} = 14$ %, 11–30 %) (Fig. 4, Data S1). Among biogeographic realms, a high number of species threatened by hunting are concentrated in Old World realms, which span from the Palearctic to the Indomalayan and peak in the Australasian region (Fig. 3). A higher proportion of hunting is observed for large-bodied and endemic species (e.g., island and geopolitically endemic) (Fig. 4) compared to their common or more wide-ranging counterparts. Larger and threatened species are more vulnerable to hunting (Threatened: MWU test = 6826, $P < 0.0001$; Non-threatened: MWU test = 27,447, $P < 0.0001$) (Fig. 2A). Although species with narrower range distributions are more prone to hunting, the threat had a minimal impact (Threatened: MWU test = 11,653, $P = 0.539$; Non-threatened: MWU test = 38,172, $P = 0.04$) (Fig. 2B). However, in terms of roosting habits and strategies, hunted species generally roost in foliage and showed a higher risk of extinction compared to other groups (Fig. 4).

We then analysed the drivers of the risk of hunting for global bats (*see* Table 1). Larger body mass consistently showed a positive relationship to species hunting risks ($\beta = 2.183$, $P < 0.001$). Hunting risk is greater in larger bats, which are predominantly in the Old World tropics (Fig. 5). Furthermore, the trophic levels of the species showed significant effects on hunting risks, but herbivores ($\beta = 2.690$, $P < 0.001$) showed a greater difference in effects compared to predators ($\beta = 1.733$, $P < 0.001$). Meanwhile, contrary to our expectations, the geographical range of the species was not significantly associated with hunting risk. However, in terms of endemism levels, only island endemism showed a significant association with hunting ($\beta = 1.094$, $P < 0.001$). Between roosting specialisation (i.e., number of roost habitat use) and sociality, the former had only shown a significant link with species risk to hunting, since species with a more generalist roosting habit are more prone to the threat ($\beta = 0.030$, $P = 0.001$). The increase in the number of threats showed a positive relationship with hunting probability ($\beta = 0.444$, $P < 0.001$). Furthermore, the probability of hunting is significant in all categories of threat and is higher in species threatened with habitat modification (63 %), followed by direct anthropogenic threats (39 %), stochastic threats (19 %) and biotic threats (10 %).

3.4. Regional socioeconomic factors in hunting and extinction risks

Overall, the richness of geopolitically endemic and threatened species hunted differed significantly between biogeographic realms, with the highest concentration in the Asian and African regions (Figs. 6A and B, 7). Furthermore, the richness of endemic and threatened species showed significant positive correlations with the number of hunted species (Spearman's ρ: endemic = 0.671, $P < 0.001$; threatened = 0.616, $P < 0.001$) (Figs. 6C and 7). We then examined the socioeconomic drivers of hunting on a global scale (Table 3). A lower percent national protected area ($\beta = -0.288$, $P = 0.008$) but increased forest cover

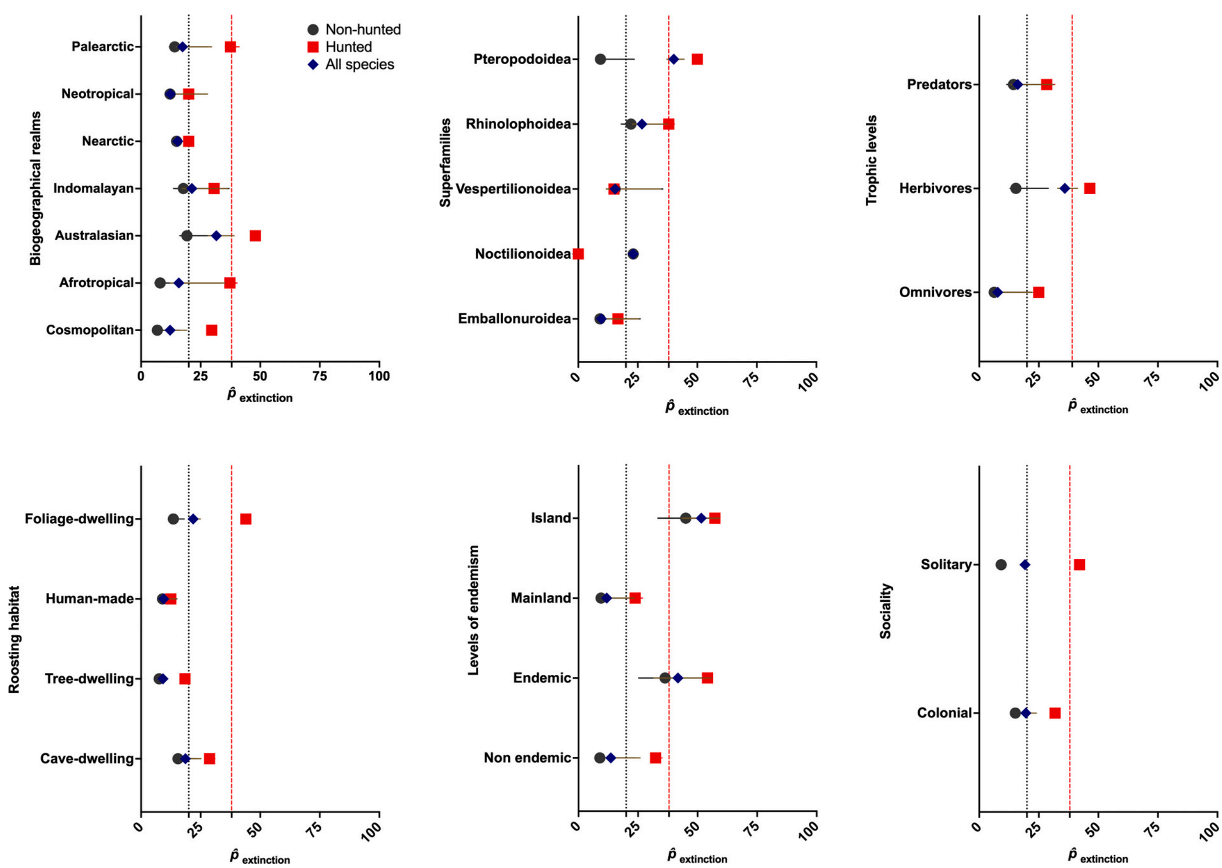

Fig. 4. Comparative proportions of extinction proportions ($\hat{p}_{\text{extinction}}$) of hunted and non-hunted species across taxonomic and ecological factors. The dashed lines indicates average global extinction risk of hunted species and dotted lines indicates global average of extinction risk for all bat species. The complete values for all scales are supplemented by Data S1.

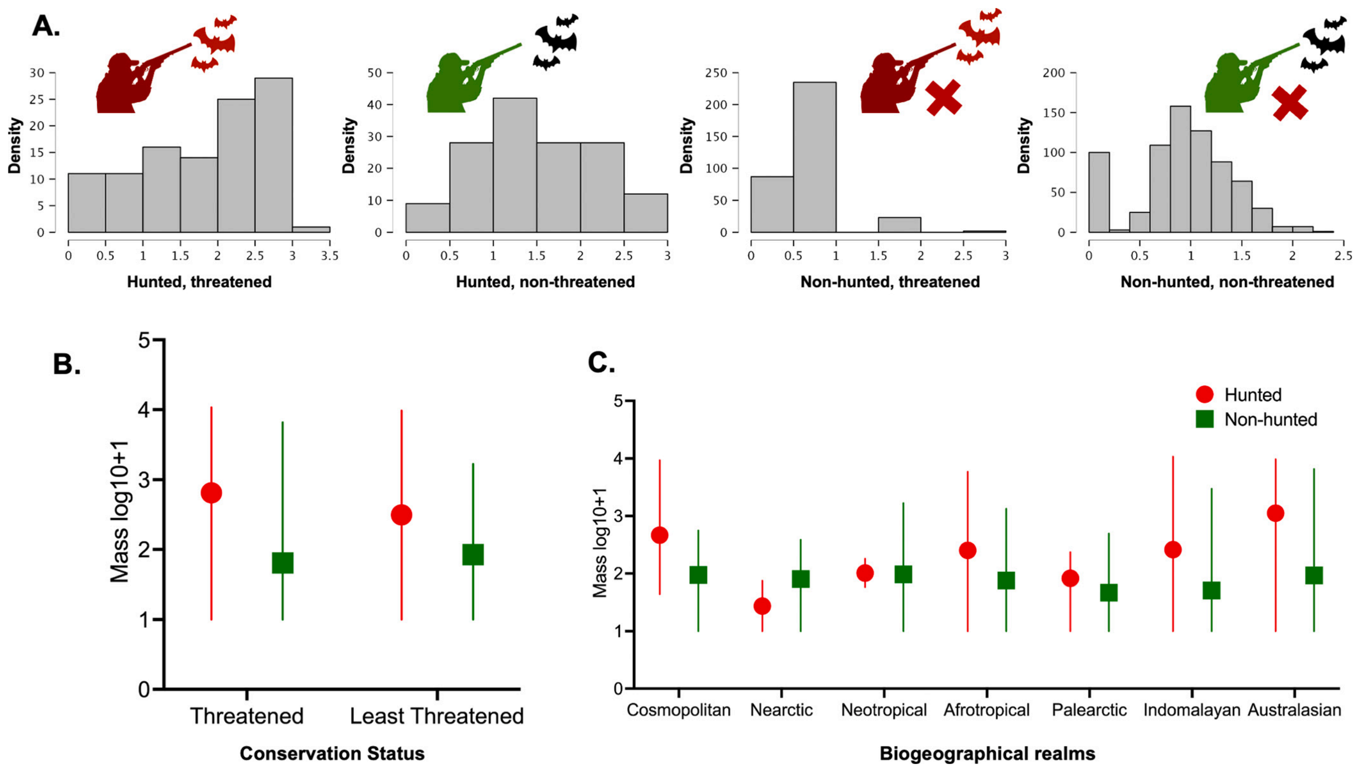

Fig. 5. Comparison of the frequency distribution of species based on mass (in grams) between hunting risk (A) and the means between the hunted and non-hunted species compared across threatened status (B) and mass of the species within the biogeographical range (C).

percentage ($\beta = 0.922$, $P < 0.001$) is linked to a higher number of species hunted. Furthermore, a higher total population ($\beta = 0.849$, $P < 0.001$), livestock production ($\beta = 0.005$, $P < 0.001$), but lower GNI per capita ($\beta = -0.937$, $P < 0.001$) predicts the richness of the species hunted per country. Separate GLM results showed that the number of hunted species and all socioeconomic variables except the percentage of national protected areas are related to the number of threatened species per country (Table 4).

4. Discussion

4.1. Worldwide extent of bat hunting

Hunting is a major threat that affects bats worldwide (Frick et al., 2020), but the extent of this threat requires further research (Mildenstein et al., 2016). Furthermore, the level of threat for bats is often underestimated compared to other mammal assessments (Ripple et al., 2016). By combining previously published syntheses (e.g., (Mickleburgh et al., 2009; Mildenstein et al., 2016; O'Shea et al., 2016; Tackett et al., 2022)) and the IUCN redlist database, 19 % or 254 species of 1320 species are threatened by hunting and harvesting around the world. Our assessment shows that there are more species vulnerable to hunting than the previous estimates of Mildenstein et al. (2016), which recorded 167 species (13 % of bats worldwide); however, these are lower compared to the estimates (27 out of 942 species, 3 %) of Ripple et al. (2016), which compared all mammals. However, the trend found in previous reports is consistent with the high spatial vulnerability of hunting in the Old World tropics of Indomalayan, Afrotropical and Australasian countries, including Oceanic Island countries, where the highest concentration of hunted bats (i.e., species richness) is observed. This pattern is also consistent with the review by O'Shea et al. (2016) where the highest mortality recorded by intentional hunting (i.e., hunting) is in Asia, Africa, and the oceanic islands. Although bat diversity is higher in the Neotropics, the mean body size of Neotropical bats is relatively small (2.4 to 167 g) compared to the Paleotropical regions (2.1 to 1075 g) (i.e., Paleotropical fruit bats can be much larger than Neotropical species), and these physical factors, combined with social factors, may underlie the observed patterns. Body mass strongly increases the hunting risk for many species. Higher hunting rates in the Old World tropics may also explain the higher risk of extinction of numerous species, particularly pteropodids in the region, primarily driven by direct human impacts (Aziz et al., 2021; Fritz et al., 2009a, 2009b; Mildenstein et al., 2016).

4.2. Influence of traits on hunting risk

The influence of increasing body mass is significant and strongly related to the disparity of bat hunting across biogeographical realms, taxonomic, and trophic levels (Fritz et al., 2009a, 2009b; Jones et al., 2003). A high proportion of species were hunted from the superfamilies of large-bodied Pteropodoidea and Rhinolopoidea and between herbivorous species. Furthermore, species hunted for in these taxonomic and functional groups have an elevated risk of extinction compared to other assessed groups. Our findings are consistent with those of Atwood et al. (2020), who stated that herbivores are at greater risk of extinction compared to predators due to higher hunting pressures. Hunting for larger bat species has an increased impact on population loss and a lower reproductive rate in many larger species (Cardillo et al., 2005; Collen et al., 2011). We expected colonial species to be more prone to hunting due to their visibility, but we did not find significant effects of sociality on hunting risk, and this may be explained by the fact that most colonial species belong to smaller species of bats such as Vespertilionoidea (6 %) and Emballonuroidea (7 %), which are the least hunted. However, species with diverse roosting habitats (i.e., generalists) and species that roost in tree foliage and caves have an elevated risk of being hunted. Hunting in these habitats is a major threat to global cave-dwelling bats because caves are easy to locate and hunt in (Phelps et al., 2016; Tanalgo et al., 2022). Larger herbivorous species, such as pteropodids, that roost in tree foliage are particularly easy to hunt due to their predictable

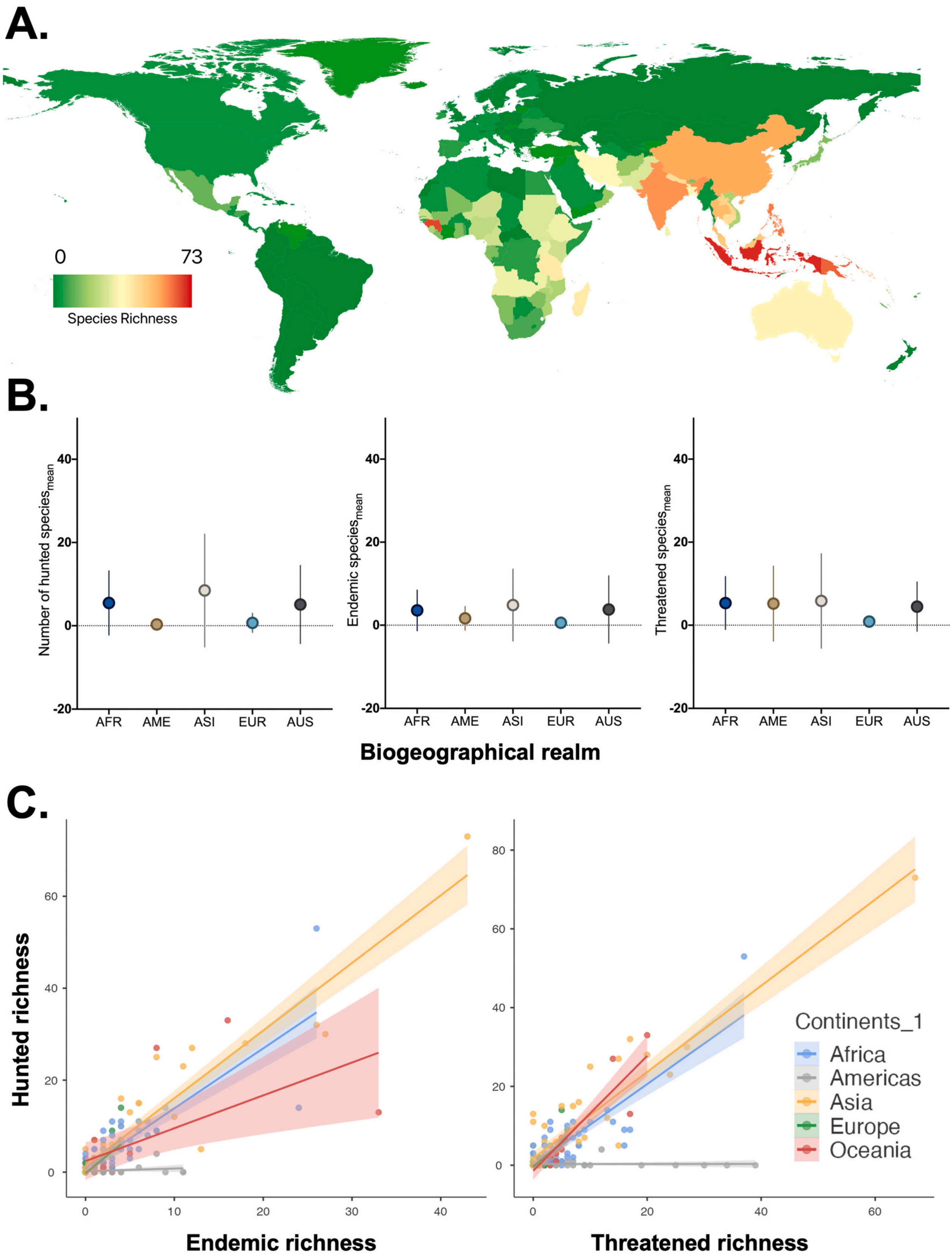

Fig. 6. Richness distribution of hunted, endemic and threatened species for global species (A) and comparison across biogeographical realms (B). Correlation between the number of endemic and threatened species to the number of hunted species (C).

A.

County	Hunted species	Threatened species	Endemic species
Indonesia	1	1	1
Guinea	2	2	3
Papua NG	3	5	7
Philippines	4	7	3
India	5	3	2
China	6	5	6
Solomon Islands	7	9	10
Thailand	7	8	8
Myanmar	9	11	10
Malaysia	10	4	9
Lao PDR	11	12	14
Cambodia	12	14	12
Nepal	12	13	12
Madagascar	14	10	5
Tanzania	14	21	14

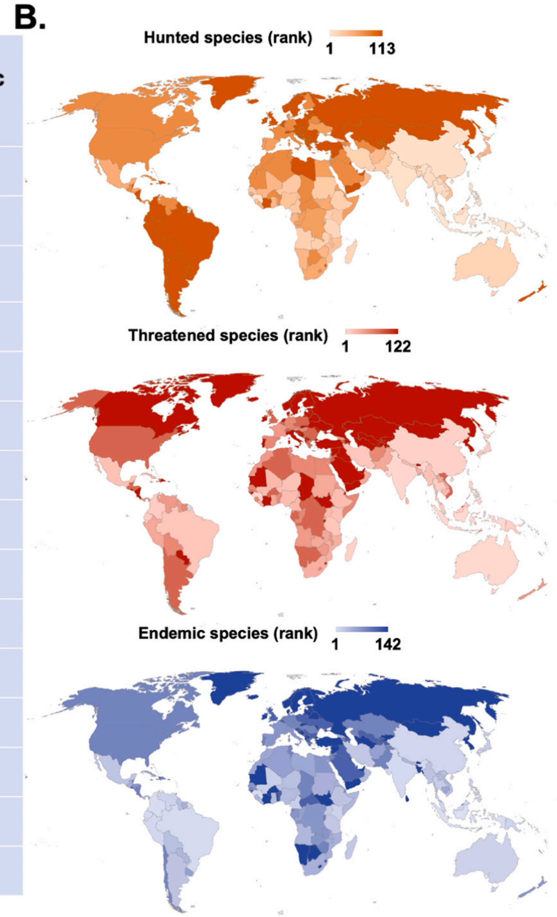

Fig. 7. The top fifteen countries ranked in terms of hunted species and their corresponding rank in terms of threatened and endemic (A). Map of country rank in terms of richness of hunted, threatened, and endemic species (B). Complete ranks are provided in Data S2.

Table 3
Results of the best generalised binomial linear model (GLM) explaining the hunting risks of bat species worldwide.

Explanatory variable	Coefficient (β)	SE	*P*
(Intercept)	−1.746	0.223	<0.001
Biotic variables			
Body mass (g, $_{\log10+1}$)	2.183	0.265	<0.001
Herbivores (omnivores)	2.690	0.513	<0.001
Predators (omnivores)	1.733	0.490	<0.001
Degree of specialisation	0.030	0.010	0.001
Sociality (colonial)	0.034	0.222	0.879
Geographical variables			
Distribution range ($_{\log10+1}$)	0.216	0.184	0.242
Geopolitical endemism (endemic)	−0.029	0.259	0.913
Island endemism (island)	1.094	0.281	<0.001
Conservation status variables			
Threatened status (threatened)	0.071	0.282	0.802
Number of threats	0.444	0.073	<0.001

Table 4
Results of the Poisson generalised linear model (GLM) explaining the number of bat species hunted (A) and the number of threatened species (B) per country. All socioeconomic and environmental variables were included in the model.

Explanatory variable	Coefficient (β)	SE	*P*
(A) Hunted species richness			
(Intercept)	0.856	0.056	<0.001
Habitat protection variables			
% forest cover ($\log_{10}$)	0.992	0.0960	<0.001
% protected area ($\log_{10}$)	−0.288	0.108	0.001
Human pressure variables			
Total population ($\log_{10}$)	0.849	0.045	<0.001
GNI per capita ($\log_{10}$)	−0.937	0.070	<0.001
Livestock production index	0.005	0.001	<0.001
(B) Threatened species richness			
(Intercept)	1.215	0.045	<0.001
Habitat protection variables			
% forest cover ($\log_{10}$)	0.551	0.088	<0.001
% protected area ($\log_{10}$)	−0.037	0.103	0.719
Human pressure variables			
Total population ($\log_{10}$)	0.558	0.044	<0.001
GNI per capita ($\log_{10}$)	−0.278	0.062	<0.001
Number of hunted species	0.030	0.002	<0.001

roosting patterns, roosting visibility, and recognisable foraging grounds in flowering and fruiting trees. Herbivores (i.e., frugivorous) forage in fruit orchards and plantations, increasing the risk of human conflict and hunting (Aziz et al., 2021, 2016). Bat predation led to intentional killings and culling of many bat populations; for example, fruit bats in Mauritius are being culled due to the purported consumption of lychee (Florens, 2016b; Florens and Baider, 2019). Although there is some evidence that culling is not an effective measure to mitigate fruit depredation, bat culling persists in some regions (Florens, 2015).

Geographic range and geopolitical endemism do not have significant effects on the risk of being hunted by species, although it may increase the impact of hunting on species survival, which is not surprising, as other factors are likely to have a greater influence (Collen et al., 2011). On a global scale, analysis of the interplay of threats to cave-dwelling bats showed that the narrow geographical range is only significantly related to land use-related threats and did not show effects on hunting (Tanalgo et al., 2022). However, island endemism showed a positive link to hunting, with 19 % of all species being island-endemic and 47 % of them at risk of hunting. Island endemism is a significant factor in the risk of hunting species because large pteropodid bats are more likely than other species to be isolated on islands and since the majority (~80 %) of hunted species are island-endemic fruit bats (family Pteropodidae), for example, large flying foxes (*Acerodon* and *Pteropus* species) are at increased risk (Aziz et al., 2021; Conenna et al., 2017; Vincenot et al., 2017). Island endemics are apparently at higher risk compared to species distributed in continental areas, due to their limited distribution and ability to rapidly move from one habitat to another (Conenna et al., 2017), which further increases their risk from habitat change and stochastic threats such as typhoons in island territories is also increasing (Jones et al., 2010).

4.3. Other co-occurrent threats

Changes and modifications in land use, such as deforestation and agricultural conversion, are major threat that affects about 30–43 % of the hunted species. Deforestation increases the vulnerability of species to hunting by decreasing the foraging habitat and home ranges and increasing species visibility and contact with hunters, and this has been observed in birds (Sreekar et al., 2015) and mammals (Benítez-López et al., 2019). Distance from human settlement and the accessibility to wildlife also increase the risk of hunting (Benítez-López et al., 2017; Peres and Lake, 2003).

Island endemic species are more prone to extinction due to their limited geographic range distribution and increased isolation, thus more vulnerable to exploitation and other threatening processes (Conenna et al., 2017; Esselstyn et al., 2006; Fritz et al., 2009a, 2009b; Jones et al., 2003; Purvis et al., 2000; Vincenot et al., 2017). In oceanic islands such as the Philippines, bats are a good source of meat because they are abundant, easy to find, and harvest (Fig. 8). In the Philippines, locals from rural areas hunt bats almost all year due to their abundance in caves and forested areas (Paz and Gonzalez, 2021; Scheffers et al., 2012; Tanalgo et al., 2016) (Fig. 8). In Madagascar, Malagasy people hunt bats as alternative meat in periods when food resources are scarce (Jenkins and Racey, 2008). Similarly, on Niue Island in the South Pacific Ocean, populations of *Pteropus tonganus* have declined since the island was colonised by human settlers from neighbouring territories, where extensive hunting occurs during famine and after hurricanes, which drives the population to extinction (Brooke and Tschapka, 2002). The predicted increase in the occurrences of extreme climate-related events puts more species from islands with a smaller population at risk of total extinction (Sherwin et al., 2013). A historical report from American Samoa showed a drastic decline of 80–90 % in the population of two species of *Pteropus* on the island after an extreme hurricane and over-hunting (Craig et al., 1994). Similarly, in the Pacific Islands of Guam and Rota, a 32 %–70 % decrease in the population of Mariana fruit bats (*Pteropus mariannus*) after a severe typhoon in 2002–2003, with a 34 % increase in bat harvesting in this period due to a lack of food sources

Fig. 8. Bats are mainly hunted for food and subsistence. Flying foxes are an easy target for locals in the Philippines due to their visibility and as meat source (A and B). Some hyperabundant cave-dwelling bats, such as *Rousettus amplexicaudatus*, are also hunted by hundreds to thousands of individuals from their roosting habitats (C). Insectivorous bats that roost in coconut foliage are also hunted for food (D)(Photo credits: A. N.K. Novillo, B. J. Rafael, C. J.A. Mangiging, and D. A.R. Agduma).

(Esselstyn et al., 2006).

4.4. Socioeconomic factors drive bat hunting

Socioeconomic elements have major implications for hunting risk (Duffy et al., 2016; O'Connor et al., 2003; Price and Gittleman, 2007; Ripple et al., 2016), but managing these pressures requires further work (Benítez-López et al., 2017). Hunting often occurs in unprotected areas such as many caves, as it is also simpler to hunt wildlife species in areas where statutory regulations are absent or not enforced, or in more accessible areas such as major towns and roads. In the tropics, hunted areas have shown drastic declines in the population of mammals (~58 %) and birds (~83 %) compared to areas without hunting (Benítez-López et al., 2017). About 60 % of tropical forests are at least 10 km from human populations, making much of the forest-dependent wildlife, including bats, more vulnerable to hunting. Predictions from previous studies showed that around 47 % of the remaining tropical forest areas are defaunated as a consequence of hunting, with approximately 50 % declines in wildlife population within 3.5 % of forested areas in the tropics (Benítez-López et al., 2019). Hunting is even higher in regions such as Africa, where hunting occurs in at least 52 % of forested areas, 62 % of wilderness areas, and almost a quarter (~20 %) of its protected areas (van Velden et al., 2020; Zyambo et al., 2022). Furthermore, in countries such as Indonesia and the Philippines, where deforestation is expanding for plantations, the hunting risk in these countries is likely to persist (Luskin et al., 2014; Tanalgo and Hughes, 2019). In addition to habitat protection variables, human pressure variables have also been shown to affect species risk from hunting. Bat hunting is probably much higher in countries with developing economies as measured by Gross National Income (GNI). Several studies show how low GNI and hunting risk are correlated (see, Price and Gittleman, 2007). Poverty, increasing population, and increasing agricultural exports reduce access to affordable local foods, causing rural people to exploit wildlife resources for food and trade (Nielsen, 2006; Ripple et al., 2016; Scheffers et al., 2012). In many tropical countries, bats are hunted primarily for food, medicine, and hunting sports and rarely for commercial trade (Mildenstein et al., 2016; Scheffers et al., 2012; Tanalgo, 2017) but Sheherazade and Tsang (2015) recorded bat bushmeat trade at around 500 metric tons annually in some areas of North Sulawesi in Indonesia. Furthermore, the sale of bats, such as *Kerivoula picta*, and other bats as ornaments is also primarily sourced from the tropics, where there are greater diversity of species but fewer protective measures (Chaber et al., 2021; Lee et al., 2015). Furthermore, we found that livestock production is related to an increased number of hunted bats per country. Reliance of rural populations on livestock and meat production could potentially increase the risk of wildlife hunting, particularly, when livestock production decreases, people will shift to an alternative source of meat increasing demand for bushmeat (Keane et al., 2005; Rogan et al., 2018). Many large-bodied bat species aggregate in accessible roosting colonies and are thus easy to hunt from their roost sites, making them an ideal alternative to livestock meat (Mildenstein et al., 2016; Paz and Gonzalez, 2021; Scheffers et al., 2012). Human-wildlife conflict between bats and livestock production is another important angle for the observed relationship, as bats are often perceived negatively as pest and disease spreaders by livestock raisers and would persecute bat colonies near their farms (Reid, 2016; Shapiro et al., 2020). However, it should be noted that species evaluated today are those that survived potentially higher former pressures in an era before the import of food, and in certain parts of the world archaeological data shows that bats were a major source of protein on otherwise depauperate islands (Hawkins et al., 2016; Lavery and Fasi, 2019), but this has changed with increased import of foods (Haden, 2009). This has driven the extinction of at least four pteropodid species in Micronesia (Vincenot et al., 2017) and up to 27 that have become at least locally extinct in the West Indies with hunting possibly playing a significant role (Morgan, 2001; Soto-Centeno and Steadman, 2015), and pressure on islands is of course high given the small population size and lack of adjacent populations for recovery (Sheherazade and Tsang, 2018; Wiles and Brooke, 2009).

Concerns about the effects of bat hunting on public health are growing, as bat hunting for consumption is widespread worldwide (Mildenstein et al., 2016; Rocha et al., 2021a) and the continuous encroachment on their habitats and the risk of people being exposed to new zoonotic diseases also increases (Rulli et al., 2021; White and Razgour, 2020). This includes under-quantified bat hunting even in regions where bats are known to host coronaviruses closely related to SARS-CoVs (Zhou et al., 2021, 2020, A. Hughes, Pers. obs.). The reliance on wild meat among low-income households and rural populations near roosting sites may continue with slow economic growth, and the lack of a persistent source of subsistence poses a much greater threat to the emergence of zoonotic diseases, which could potentially lead to another global pandemic if the solution remains unsolved. Balancing economics and conservation is challenging, especially since hunting is more common in lower-income regions, where diversity, particularly of pteropodids is higher; therefore, interventions to reduce bat hunting should include exploring alternatives such as increasing access to domestic meat resources, the provision of additional source income generation, and more investments in the rural economy, raising awareness of ecosystem services and the potential for bat disease transmission (MacFarlane and Rocha, 2020; Tanalgo and Hughes, 2021).

4.5. Impacts on bat ecosystem services

More than half (~55 %) of the hunted species are fruit bats from the Old World tropics. These bat groups maintain numerous vital ecosystem services for the economy by sustaining gene flow among plant communities (Dick et al., 2008; Dunphy et al., 2004). There are around 1072 plant species that are currently known to depend on Old World fruit bats, with strong evidence for 21 and 311 plant species dependent on 16 and 29 bat species for pollination and seed dispersal, respectively (Aziz et al., 2021). Bats are also responsible for the pollination of economically important plant species such as *Durio* in Southeast Asia (Aziz et al., 2017; Sritongchuay et al., 2016). Fruit bats are also more efficient seed dispersers in terms of distance compared to other frugivores, which range from 400 m for small fruit bats to 7.2 km for larger fruit bats (e.g., flying foxes) (Aziz et al., 2021). Incessant bat hunting pressure combined with other threatening processes could jeopardize ecosystem service provision and ecosystem functioning (Bello et al., 2015; Gardner et al., 2019; Harrison et al., 2013). Reduction in populations can affect the dynamics of ecosystem processes such as vegetation alteration due to loss of seed dispersers and plant pollinators, especially in island systems (Muller-Landau, 2007), reduced forest regeneration after loss or degradation (Harrison et al., 2013; Hurme et al., 2022), biogeochemical processes, and energy transfer dynamics (i.e., cave-dwellings to cave invertebrates dependent on bat guano for nutrients) (Bello et al., 2015; Benítez-López et al., 2019; Gardner et al., 2019). More effort should be put into identifying the impacts of hunting on bat ecosystem services, and the interplay of other threatening processes to increase hunting risk.

4.6. Implications to global bat conservation

The extent of hunting pressure among bats is underestimated, and the drivers of hunting are unclear and unexplored. Bat hunting widely occurs in areas where bat biodiversity is also high. Approximately a quarter (~24 %) of threatened bat species are under pressure from hunting, and other threats and socioeconomic status exacerbate the risk. We found that larger bats, herbivores, and island endemics are more prone to hunting, suggesting that threat vulnerability can be trait dependent. Globally, bats are hunted and threatened equally as other wildlife species, but 'charismatic species' such as megafaunal species tend to receive an overwhelming proportion of these funds under the guise of being 'umbrella' or 'indicator' species (Feldhamer et al., 2002; Gerber, 2016; Wang et al., 2021). Many studies also show that funding often neglects species deemed less charismatic, such as bats (Gerber, 2016; Macdonald et al., 2015; Wang et al., 2021). For example, Ripple et al. (2016) focused on the hunting of all mammalian taxonomic groups, but only recorded 27 (3 %) bat species facing hunting as a threat, which is very low compared to the actual extent of species threatened by hunting (Mildenstein et al., 2016 and this study), and while we find evidence for hunting in 254 species (19 % of global bats) with 58 % are in the least threatened categories. The expert-based IUCN redlist can also help reduce the risk by alleviating the conservation status of widely hunted genera (e.g., *Rousettus* and *Eidolon*). They are intensely hunted throughout their range, but remain under-protected due to their least threatened category in the redlist or non-endemic, which are often not prioritised in national conservation actions (Kamins et al., 2011; Tanalgo and Hughes, 2019). A good example of such a case is the *Pteropus vampyrus*, where hunting is the single largest threat to the species and facing severe extinction risk across its range (extinct in Singapore and near-extinction in Vietnam), but the species remained under the least concerned category and has lacked sufficient updates of its conservation status for decades (S. Abdul-Aziz, Pers. com). If the assignment of lower conservation categories for many bats that face more threats continues to persist, a large proportion of global bats (e.g., 86 % of the hunted pteropodids are in the categories) will continue to be under-protected and consequently expected to face extinction over the next decades.

Although our data is likely to be incomplete (i.e., local, and national-level data for species hunting pressure remains limited, and requires more work), the data and relationships between species ecology and economic status where they occur highlight the impacts of a specific threatening process to underrepresented taxa such as bats. Countries with lower protected areas and lower income are more likely to have hunted for a higher proportion of species (see Fig. 6). This trend is not surprising and parallels that of Ripple et al. (2016) for global mammals more widely, as socioeconomic factors disproportionately affect the national capacity to protect biodiversity (Doi and Takahara, 2016; Holland et al., 2009). Conversely, capacity and funding limitations can challenge effective conservation. In addition, bat hunting is driven by several factors, including use for subsistence, beliefs, and other cultural dimensions (Fig. 8). This facet of bat conservation needs careful attention and understanding the extent of hunting and its impacts on the population is a key important step in balancing human needs and conservation. Therefore, science-based policies that balance elements of social, economic factors, and biodiversity conservation should be one of the agendas of national policymakers to protect not only the bat population but also all other wildlife to ensure that their ecosystem services are maintained. Mainstreaming bat ecosystem services and their cultural values (e.g., Low et al., 2021; Rocha et al., 2021b) would further benefit public support towards bat conservation and protection.

CRediT authorship contribution statement

Krizler Cejuela. Tanalgo: Conceptualization, Materials and Methods, Formal analysis, Validation, Investigation, Data Curation, Writing – original draft, Writing – review & editing, Vizualisation, Project administration. **Tuanjit Sritongchuay:** Conceptualization, Data Curation, Writing – original draft, Writing – review & editing. **Angelo Rellama Agduama:** Formal analysis, Data Curation, Writing – original draft, Writing – review & editing. **Kier Celestial Dela Cruz:** Materials and Methods, Data Curation, Writing – original draft, Writing – review & editing. **Alice C. Hughes:** Conceptualization, Materials and Methods, Formal analysis, Validation, Investigation, Data Curation, Writing – original draft, Writing – review & editing, Visualization, Project administration.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

Data availability

Data will be made available on request.

Acknowledgments

We would like to thank editors and the two anonymous reviewers for their insightful comments that greatly helped improved the quality of the manuscript. We are also grateful to Dr. Sheema Abdul-Aziz (RIMBA, Malaysia) for the useful discussion and materials that were valuable to the direction of the work. This work was a part of the Doctoral project of KCT at the Chinese Academy of Sciences, P.R. China, and a student fellowship supported by the Zukunftskolleg Connect Fellowship (2020−2021) and the Centre for Advanced Study of Collective Behaviour at the University of Konstanz, Germany.

References

Arponen, A., 2012. Prioritizing species for conservation planning. Biodivers. Conserv. 21, 875–893. https://doi.org/10.1007/s10531-012-0242-1.
Atwood, T.B., Valentine, S.A., Hammill, E., McCauley, D.J., Madin, E.M.P., Beard, K.H., Pearse, W.D., 2020. Herbivores at the highest risk of extinction among mammals, birds, and reptiles. ScienceAdvances 6, eabb8458. https://doi.org/10.1126/sciadv.abb8458.
Aziz, S., Clements, G.R., McConkey, K.R., Sritongchuay, T., Pathil, S., Yazid, M.N.H.A., Campos-Arceiz, A., Forget, P.-M., Bumrungsri, S., 2017. Pollination by the locally endangered island flying fox (Pteropus hypomelanus) enhances fruit production of the economically important durian (Durio zibethinus). Ecol. Evol. 7, 8670–8684. https://doi.org/10.1002/ece3.3213.
Aziz, S.A., McConkey, K., Tanalgo, K., Sritongchuay, T., Low, M.-R., Yong, J.Y., Mildenstein, T.L., Nuevo-Diego, C.E., Lim, V.-C., Racey, P.A., 2021. The critical importance of Old World fruit bats for healthy ecosystems and economies. Front. Ecol. Evol. 9 https://doi.org/10.3389/fevo.2021.641411.
Aziz, S.A., Olival, K.J., Bumrungsri, S., Richards, G.C., Racey, P.A., 2016. The conflict between pteropodid bats and fruit growers: species, legislation and mitigation. In: Voigt, C.C., Kingston, T. (Eds.), Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer International Publishing, Cham, pp. 377–426. https://doi.org/10.1007/978-3-319-25220-9_13.
Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., Peres, C.A., Ovaskainen, O., Jordano, P., 2015. Defaunation affects carbon storage in tropical forests. Sci. Adv. 1, e1501105 https://doi.org/10.1126/sciadv.1501105.
Benítez-López, A., Alkemade, R., Schipper, A.M., Ingram, D.J., Verweij, P.A., Eikelboom, J.A.J., Huijbregts, M.A.J., 2017. The impact of hunting on tropical mammal and bird populations. Science 356, 180–183. https://doi.org/10.1126/science.aaj1891.
Benítez-López, A., Santini, L., Schipper, A.M., Busana, M., Huijbregts, M.A.J., 2019. Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. PLoS Biol. 17, e3000247 https://doi.org/10.1371/journal.pbio.3000247.
Bland, L.M., Collen, B., Orme, C.D.L., Bielby, J., 2015. Predicting the conservation status of data-deficient species. Conserv. Biol. 29, 250–259. https://doi.org/10.1111/cobi.12372.
Brierley, L., Vonhof, M.J., Olival, K.J., Daszak, P., Jones, K.E., 2016. Quantifying global drivers of zoonotic bat viruses: a process-based perspective. Am. Nat. 187, E53–E64. https://doi.org/10.1086/684391.
Brooke, A.P., Tschapka, M., 2002. Threats from overhunting to the flying fox, Pteropus tonganus, (Chiroptera: Pteropodidae) on Niue Island, South Pacific Ocean. Biol. Conserv. 103, 343–348. https://doi.org/10.1016/S0006-3207(01)00145-8.
Brum, F.T., Graham, C.H., Costa, G.C., Hedges, S.B., Penone, C., Radeloff, V.C., Rondinini, C., Loyola, R., Davidson, A.D., 2017. Global priorities for conservation across multiple dimensions of mammalian diversity. Proc. Natl. Acad. Sci. U. S. A. 114, 7641–7646. https://doi.org/10.1073/pnas.1706461114.
Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. Science 309, 1239–1241. https://doi.org/10.1126/science.1116030.
Caro, T., Darwin, J., Forrester, T., Ledoux-Bloom, C., Wells, C., 2012. Conservation in the anthropocene. Conserv. Biol. 26, 185–188. https://doi.org/10.1111/j.1523-1739.2011.01752.x.
Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253 https://doi.org/10.1126/sciadv.1400253.
Cerri, J., Mori, E., Ancillotto, L., Russo, D., Bertolino, S., 2022. COVID-19, media coverage of bats and related web searches: a turning point for bat conservation? Mammal Rev. 52, 16–25. https://doi.org/10.1111/mam.12261.
Chaber, A.-L., Amstrong, K.N., Wiantoro, S., Xerri, V., Caraguel, C., Boardman, W.S.J., Nielsen, T.D., 2021. Bat E-commerce: insights into the extent and potential implications of this dark trade. Frontiers in veterinaryScience 8.

Collen, B., McRae, L., Deinet, S., De Palma, A., Carranza, T., Cooper, N., Loh, J., Baillie, J.E.M., 2011. Predicting how populations decline to extinction. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 366, 2577–2586. https://doi.org/10.1098/rstb.2011.0015.
Conenna, I., Rocha, R., Russo, D., Cabeza, M., 2017. Insular bats and research effort: a review of global patterns and priorities. Mammal Rev. 47, 169–182. https://doi.org/10.1111/mam.12090.
Corlett, R.T., 2015. The anthropocene concept in ecology and conservation. Trends Ecol. Evol. 30, 36–41. https://doi.org/10.1016/j.tree.2014.10.007.
Craig, P., Trail, P., Morrell, T.E., 1994. The decline of fruit bats in American Samoa due to hurricanes and overhunting. Biol. Conserv. 69, 261–266. https://doi.org/10.1016/0006-3207(94)90425-1.
Dick, C.W., Hardy, O.J., Jones, F.A., Petit, R.J., 2008. Spatial scales of pollen and seed-mediated gene flow in tropical rain Forest trees. Tropical Plant Biol. 1, 20–33. https://doi.org/10.1007/s12042-007-9006-6.
Doi, H., Takahara, T., 2016. Global patterns of conservation research importance in different countries of the world. PeerJ 4, e2173. https://doi.org/10.7717/peerj.2173.
Duffy, R., St John, F.A.V., Büscher, B., Brockington, D., 2016. Toward a new understanding of the links between poverty and illegal wildlife hunting. Conserv. Biol. 30, 14–22. https://doi.org/10.1111/cobi.12622.
Dunphy, B.K., Hamrick, J.L., Schwagerl, J., 2004. A comparison of direct and indirect measures of gene flow in the bat-pollinated tree Hymenaea courbaril in the dry Forest life zone of southwestern Puerto Rico. Int. J. Plant Sci. 165, 427–436. https://doi.org/10.1086/382802.
Esselstyn, J.A., Amar, A., Janeke, D., 2006. Impact of post-typhoon hunting on Mariana fruit bats (Pteropus mariannus)1. pasc 60, 531–539. https://doi.org/10.1353/psc.2006.0027.
Faurby, S., Davis, M., Pedersen, R.Ø., Schowanek, S.D., Antonelli, A., Svenning, J.-C., 2018. PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. Ecology 99. https://doi.org/10.1002/ecy.2443, 2626–2626.
Feldhamer, G., Whittaker, J., Monty, A.-M., Weickert, C., 2002. Charismatic mammalian megafauna: public empathy and marketing strategy. J. Pop. Cult. 36, 160–167. https://doi.org/10.1111/1540-5931.00037.
Florens, F.B.V., 2016a. Biodiversity law: Mauritius culls threatened fruit bats. Nature 530. https://doi.org/10.1038/530033a, 33–33.
Florens, F.B.V., 2016b. Mauritius culls threatened fruit bats. Nature 530. https://doi.org/10.1038/530033a, 33–33.
Florens, F.B.V., 2015. Flying foxes face cull despite evidence. Science 350. https://doi.org/10.1126/science.350.6266.1325-a, 1325–1325.
Florens, F.B.V., Baider, C., 2019. Mass-culling of a threatened island flying fox species failed to increase fruit growers' profits and revealed gaps to be addressed for effective conservation. J. Nat. Conserv. 47, 58–64. https://doi.org/10.1016/j.jnc.2018.11.008.
Frick, W.F., Kingston, T., Flanders, J., 2020. A review of the major threats and challenges to global bat conservation. Ann. N. Y. Acad. Sci. 1469, 5–25. https://doi.org/10.1111/nyas.14045.
Fritz, Susanne A., Bininda-Emonds, O.R., Purvis, A., 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecol. Lett. 12, 538–549.
Fritz, Susanne A., Bininda-Emonds, O.R.P., Purvis, A., 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. Ecol. Lett. 12, 538–549. https://doi.org/10.1111/j.1461-0248.2009.01307.x.
Gardner, C.J., Bicknell, J.E., Baldwin-Cantello, W., Struebig, M.J., Davies, Z.G., 2019. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. Nat. Commun. 10, 4590. https://doi.org/10.1038/s41467-019-12539-1.
Gerber, L.R., 2016. Conservation triage or injurious neglect in endangered species recovery. PNAS 113, 3563–3566. https://doi.org/10.1073/pnas.1525085113.
GraphPad version 8, n.d. GraphPad Version 8, n.d. GraphPad Software, Inc., San Diego, CA [WWW Document]. URL https://www.graphpad.com/ (accessed 7.31.21).
Haden, R., 2009. Food culture in the Pacific Islands. ABC-CLIO.
Harfoot, M.B.J., Johnston, A., Balmford, A., Burgess, N.D., Butchart, S.H.M., Dias, M.P., Hazin, C., Hilton-Taylor, C., Hoffmann, M., Isaac, N.J.B., Iversen, L.L., Outhwaite, C.L., Visconti, P., Geldmann, J., 2021. Using the IUCN red list to map threats to terrestrial vertebrates at global scale. Nat. Ecol. Evol. 5, 1510–1519. https://doi.org/10.1038/s41559-021-01542-9.
Harrison, R.D., Tan, S., Plotkin, J.B., Slik, F., Detto, M., Brenes, T., Itoh, A., Davies, S.J., 2013. Consequences of defaunation for a tropical tree community. Ecol. Lett. 16, 687–694. https://doi.org/10.1111/ele.12102.
Hawkins, S., O'connor, S., Kealy, S., 2016. Late quaternary hominin–bat (Chiroptera) interactions in the Asia-Pacific. Archaeol. Ocean. 51, 7–17. https://doi.org/10.1002/arco.5084.
Hayward, M.W., 2009. The need to rationalize and prioritize threatening processes used to determine threat status in the IUCN red list. Conserv. Biol. 23, 1568–1576. https://doi.org/10.1111/j.1523-1739.2009.01260.x.
Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., Carpenter, K.E., Chanson, J., Collen, B., Cox, N.A., Darwall, W.R.T., Dulvy, N.K., Harrison, L.R., Katariya, V., Pollock, C.M., Quader, S., Richman, N.I., Rodrigues, A.S.L., Tognelli, M.F., Vié, J.-C., Aguiar, J.M., Allen, D.J., Allen, G.R., Amori, G., Ananjeva, N.B., Andreone, F., Andrew, P., Ortiz, A.L.A., Baillie, J.E.M., Baldi, R., Bell, B.D., Biju, S.D., Bird, J.P., Black-Decima, P., Blanc, J.J., Bolaños, F., Bolivar-G, W., Burfield, I.J., Burton, J.A., Capper, D.R., Castro, F., Catullo, G., Cavanagh, R.D., Channing, A., Chao, N.L., Chenery, A.M., Chiozza, F., Clausnitzer, V., Collar, N.J., Collett, L.C., Collette, B.B., Fernandez, C.F.C., Craig, M.T., Crosby, M.J., Cumberlidge, N., Cuttelod, A., Derocher, A.E., Diesmos, A.C., Donaldson, J.S., Duckworth, J.W., Dutson, G., Dutta, S.K., Emslie, R.H., Farjon, A., Fowler, S., Freyhof, J., Garshelis, D.L., Gerlach, J., Gower, D.J., Grant, T.D., Hammerson, G.A., Harris, R.B., Heaney, L.R., Hedges, S.B., Hero, J.-M., Hughes, B., Hussain, S.A., M., J. I., Inger, R.F., Ishii, N., Iskandar, D.T., Jenkins, R.K.B., Kaneko, Y., Kottelat, M., Kovacs, K.M., Kuzmin, S.L., Marca, E.L., Lamoreux, J.F., Lau, M.W.N., Lavilla, E.O., Leus, K., Lewison, R.L., Lichtenstein, G., Livingstone, S.R., Lukoschek, V., Mallon, D.P., McGowan, P.J.K., McIvor, A., Moehlman, P.D., Molur, S., Alonso, A.M., Musick, J.A., Nowell, K., Nussbaum, R.A., Olech, W., Orlov, N.L., Papenfuss, T.J., Parra-Olea, G., Perrin, W.F., Polidoro, B.A., Pourkazemi, M., Racey, P.A., Ragle, J.S., Ram, M., Rathbun, G., Reynolds, R.P., Rhodin, A.G.J., Richards, S.J., Rodríguez, L.O., Ron, S.R., Rondinini, C., Rylands, A.B., Mitcheson, Y.S.de, Sanciangco, J.C., Sanders, K.L., Santos-Barrera, G., Schipper, J., Self-Sullivan, C., Shi, Y., Shoemaker, A., Short, F.T., Sillero-Zubiri, C., Silvano, D.L., Smith, K.G., Smith, A.T., Snoeks, J., Stattersfield, A.J., Symes, A.J., Taber, A.B., Talukdar, B.K., Temple, H.J., Timmins, R., Tobias, J.A., Tsytsulina, K., Tweddle, D., Ubeda, C., Valenti, S.V., Dijk, P.P.van, Veiga, L.M., Veloso, A., Wege, D.C., Wilkinson, M., Williamson, E.A., Xie, F., Young, B.E., Akçakaya, H.R., Bennun, L., Blackburn, T.M., Boitani, L., Dublin, H.T., Fonseca, G.A.B.da, Gascon, C., Lacher, T.E., Mace, G.M., Mainka, S.A., McNeely, J.A., Mittermeier, R.A., Reid, G.M., Rodriguez, J.P., Rosenberg, A.A., Samways, M.J., Smart, J., Stein, B.A., Stuart, S.N., 2010. The impact of conservation on the status of the world's vertebrates. Science 330, 1503–1509. https://doi.org/10.1126/science.1194442.
Holland, T.G., Peterson, G.D., Gonzalez, A., 2009. A cross-national analysis of how economic inequality predicts biodiversity loss. Conserv. Biol. 23, 1304–1313. https://doi.org/10.1111/j.1523-1739.2009.01207.x.
Hughes, A.C., 2017. Mapping priorities for conservation in Southeast Asia. Biol. Conserv. 209, 395–405. https://doi.org/10.1016/j.biocon.2017.03.007.
Hurme, E., Fahr, J., Network, E.M., Eric-Moise, B.F., Hash, C.T., O'Mara, M.T., Richter, H., Tanshi, I., Webala, P.W., Weber, N., Wikelski, M., Dechmann, D.K.N., 2022. Fruit bat migration matches green wave in seasonal landscapes. Funct. Ecol. 36, 2043–2055. https://doi.org/10.1111/1365-2435.14097.
International Monetary Fund (Ed.), 2009. Balance of payments and international investment position manual, 6th ed. International Monetary Fund, Washington D.C.
Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C., Baillie, J.E.M., 2007. Mammals on the EDGE: conservation priorities based on threat and phylogeny. PLOS ONE 2, e296. https://doi.org/10.1371/journal.pone.0000296.
IUCN Red List, 2021. The IUCN Red List of Threatened Species [WWW Document]. IUCN Red List of Threatened Species. https://www.iucnredlist.org/en. (Accessed 9 December 2021).
Jenkins, R.K.B., Racey, P.A., 2008. Bats as bushmeat in MadagascarMadagascar Conservation & Development, 3. https://doi.org/10.4314/mcd.v3i1.44132.
Jones, K.E., Mickleburgh, S.P., Sechrest, W., Walsh, A.L., 2010. 16. Global overview of the conservation of island bats: importance, challenges, and opportunities. In: 16. Global Overview of the Conservation of Island Bats: Importance, Challenges, and Opportunities. University of Chicago Press, pp. 496–530. https://doi.org/10.7208/9780226253312-016.
Jones, K.E., Purvis, A., Gittleman, J.L., 2003. Biological correlates of extinction risk in bats. Am. Nat. 161, 601–614. https://doi.org/10.1086/368289.
Kamins, A.O., Restif, O., Ntiamoa-Baidu, Y., Suu-Ire, R., Hayman, D.T.S., Cunningham, A.A., Wood, J.L.N., Rowcliffe, J.M., 2011. Uncovering the fruit bat bushmeat commodity chain and the true extent of fruit bat hunting in Ghana, West Africa. Biol. Conserv. 144, 3000–3008. https://doi.org/10.1016/j.biocon.2011.09.003.
Keane, A., Brooke, M.de L., Mcgowan, P.J.K., 2005. Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). Biological Conservation 126, 216–233. https://doi.org/10.1016/j.biocon.2005.05.011.
Lavery, T.H., Fasi, J., 2019. Buying through your teeth: traditional currency and conservation of flying foxes Pteropus spp. in Solomon Islands. Oryx 53, 505–512. https://doi.org/10.1017/S0030605317001004.
Lee, B.P.Y.-H., Struebig, M.J., Rossiter, S.J., Kingston, T., 2015. Increasing concern over trade in bat souvenirs from south-East Asia. Oryx 49. https://doi.org/10.1017/S0030605315000034, 204–204.
Low, M.-R., Hoong, W.Z., Shen, Z., Murugavel, B., Mariner, N., Paguntalan, L.M., Tanalgo, K., Aung, M.M., Sheherazade, Bansa, L.A., Sritongchuay, T., Preble, J.H., Aziz, S.A., 2021. In: Bane or Blessing? Reviewing Cultural Values of Bats across the Asia-Pacific Region, 41. etbi, pp. 18–34. https://doi.org/10.2993/0278-0771-41.1.18.
Luskin, M.S., Christina, E.D., Kelley, L.C., Potts, M.D., 2014. Modern hunting practices and wild meat trade in the oil palm plantation-dominated landscapes of Sumatra, Indonesia. Hum. Ecol. 42, 35–45. https://doi.org/10.1007/s10745-013-9606-8.
Macdonald, E.A., Burnham, D., Hinks, A.E., Dickman, A.J., Malhi, Y., Macdonald, D.W., 2015. Conservation inequality and the charismatic cat: Felis felicis. Glob. Ecol. Conserv. 3, 851–866. https://doi.org/10.1016/j.gecco.2015.04.006.
MacFarlane, D., Rocha, R., 2020. Guidelines for communicating about bats to prevent persecution in the time of COVID-19. Biol. Conserv. 248, 108650 https://doi.org/10.1016/j.biocon.2020.108650.
Medellin, R.A., Wiederholt, R., Lopez-Hoffman, L., 2017. Conservation relevance of bat caves for biodiversity and ecosystem services. Biological Conservation 211, 45–50. https://doi.org/10.1016/j.biocon.2017.01.012. Small Natural Features.
Mickleburgh, S., Waylen, K., Racey, P., 2009. Bats as bushmeat: a global review. Oryx 43, 217–234. https://doi.org/10.1017/S0030605308000938.
Mildenstein, T., Tanshi, I., Racey, P.A., 2016. Exploitation of bats for bushmeat and medicine. In: Voigt, C.C., Kingston, T. (Eds.), Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer International Publishing, Cham, pp. 325–375. https://doi.org/10.1007/978-3-319-25220-9_12.
Morgan, G., 2001. Patterns of extinction in West Indian Bats. In: Biogeography of the West Indies. CRC Press. https://doi.org/10.1201/9781420039481-20.

Muller-Landau, H.C., 2007. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. Biotropica 39, 372–384. https://doi.org/10.1111/j.1744-7429.2007.00290.x.
Nielsen, M.R., 2006. Importance, cause and effect of bushmeat hunting in the Udzungwa Mountains, Tanzania: implications for community based wildlife management. Biol. Conserv. 128, 509–516. https://doi.org/10.1016/j.biocon.2005.10.017.
O'Connor, C., Marvier, M., Kareiva, P., 2003. Biological vs. social, economic and political priority-setting in conservation. Ecol. Lett. 6, 706–711. https://doi.org/10.1046/j.1461-0248.2003.00499.x.
Oedin, M., Brescia, F., Vidal, E., Millon, A., 2021. Make flying-fox hunting sustainable again: comparing expected demographic effectiveness and hunters' acceptance of more restrictive regulations. Ambio. https://doi.org/10.1007/s13280-021-01630-x.
O'Shea, T.J., Cryan, P.M., Hayman, D.T.S., Plowright, R.K., Streicker, D.G., 2016. Multiple mortality events in bats: a global review. Mammal Rev. 46, 175–190. https://doi.org/10.1111/mam.12064.
Paz, S.L., Gonzalez, J.C.T., 2021. Understanding human-flying fox interactions in the agusan marsh wildlife sanctuary as basis for conservation policy interventions. J. Threat. Taxa 13, 19431–19447. https://doi.org/10.11609/jott.7466.13.11.19431-19447.
Peres, C.A., Lake, I.R., 2003. Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon Basin. Conserv. Biol. 17, 521–535. https://doi.org/10.1046/j.1523-1739.2003.01413.x.
Phelps, K., Jose, R., Labonite, M., Kingston, T., 2016. Correlates of cave-roosting bat diversity as an effective tool to identify priority caves. Biol. Conserv. 201, 201–209. https://doi.org/10.1016/j.biocon.2016.06.023.
Price, S.A., Gittleman, J.L., 2007. Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. Proceedings of the Royal Society B: Biological Sciences 274, 1845–1851. https://doi.org/10.1098/rspb.2007.0505.
Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society of London. Series B: Biological Sciences 267, 1947–1952. https://doi.org/10.1098/rspb.2000.1234.
Rainforest Rescue. Stop the Mass Slaughter of Migratory Birds! [WWW Document]. undated. https://www.rainforest-rescue.org/petitions/1151. (Accessed 11 November 2022).
Reid, J.L., 2016. Knowledge and experience predict indiscriminate bat-killing intentions among costa rican men. Biotropica 48, 394–404. https://doi.org/10.1111/btp.12279.
Richman, N.I., Böhm, M., Adams, S.B., Alvarez, F., Bergey, E.A., Bunn, J.J.S., Burnham, Q., Cordeiro, J., Coughran, J., Crandall, K.A., Dawkins, K.L., DiStefano, R. J., Doran, N.E., Edsman, L., Eversole, A.G., Füreder, L., Furse, J.M., Gherardi, F., Hamr, P., Holdich, D.M., Horwitz, P., Johnston, K., Jones, C.M., Jones, J.P.G., Jones, R.L., Jones, T.G., Kawai, T., Lawler, S., López-Mejía, M., Miller, R.M., Pedraza-Lara, C., Reynolds, J.D., Richardson, A.M.M., Schultz, M.B., Schuster, G.A., Sibley, P.J., Souty-Grosset, C., Taylor, C.A., Thoma, R.F., Walls, J., Walsh, T.S., Collen, B., 2015. Multiple drivers of decline in the global status of freshwater crayfish (Decapoda: Astacidea). Philos. Trans. R. Soc., B 370, 20140060. https://doi.org/10.1098/rstb.2014.0060.
Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P.A., Macdonald, D.W., Machovina, B., Newsome, T.M., Peres, C.A., Wallach, A.D., Wolf, C., Young, H., 2016. Bushmeat hunting and extinction risk to the world's mammals. R. Soc. Open Sci. 3, 160498 https://doi.org/10.1098/rsos.160498.
Ritchie, H., Roser, M., 2021. Biodiversity. In: Our World in Data.
Rocha, R., Aziz, S.A., Brook, C.E., Carvalho, W.D., Cooper-Bohannon, R., Frick, W.F., Huang, J.C.-C., Kingston, T., López-Baucells, A., Maas, B., Mathews, F., Medellin, R. A., Olival, K.J., Peel, A.J., Plowright, R.K., Razgour, O., Rebelo, H., Rodrigues, L., Rossiter, S.J., Russo, D., Straka, T.M., Teeling, E.C., Treuer, T., Voigt, C.C., Webala, P.W., 2021. Bat conservation and zoonotic disease risk: a research agenda to prevent misguided persecution in the aftermath of COVID-19. Anim. Conserv. 24, 303–307. https://doi.org/10.1111/acv.12636.
Rocha, Ricardo, López-Baucells, A., Fernández-Llamazares, Á., 2021. Ethnobiology of bats: exploring human-bat inter-relationships in a rapidly changing world. etbi 41, 3–17. https://doi.org/10.2993/0278-0771-41.1.3.
Rogan, M.S., Miller, J.R.B., Lindsey, P.A., McNutt, J.W., 2018. Socioeconomic drivers of illegal bushmeat hunting in a southern African savanna. Biol. Conserv. 226, 24–31. https://doi.org/10.1016/j.biocon.2018.07.019.
Rulli, M.C., D'Odorico, P., Galli, N., Hayman, D.T.S., 2021. Land-use change and the livestock revolution increase the risk of zoonotic coronavirus transmission from rhinolophid bats. Nat. Food 2, 409–416. https://doi.org/10.1038/s43016-021-00285-x.
Sagot, M., Chaverri, G., 2015. Effects of roost specialization on extinction risk in bats. Conserv. Biol. 29, 1666–1673. https://doi.org/10.1111/cobi.12546.
Scheffers, B.R., Corlett, R.T., Diesmos, A., Laurance, W.F., 2012. Local demand drives a bushmeat industry in a philippine Forest preserve. Trop. Conserv. Sci. 5, 133–141. https://doi.org/10.1177/194008291200500203.
Shapiro, H.G., Wilcox, A.S., Tate, M., Willcox, E.V., 2020. Can Farmers and Bats Co-exist? Farmer Attitudes, Knowledge, and Experiences With Bats in Belize. https://doi.org/10.26077/5WWP-SP53.
Sheherazade, Tsang, S.M., 2018. Roost of gray flying foxes (Pteropus griseus) in Indonesia and records of a new hunting threat. Diversity 10, 102. https://doi.org/10.3390/d10030102.
Sheherazade, Tsang, S.M., 2015. Quantifying the bat bushmeat trade in North Sulawesi, Indonesia, with suggestions for conservation action. Global Ecology and Conservation 3, 324–330. https://doi.org/10.1016/j.gecco.2015.01.003.
Sherwin, H.A., Montgomery, W.I., Lundy, M.G., 2013. The impact and implications of climate change for bats. Mammal Rev. 43, 171–182. https://doi.org/10.1111/j.1365-2907.2012.00214.x.
Simmons, N., Cirranello, A., 2020. BatSpecies of the World: A Taxonomic and Geographic Database. WWW Document. https://batnames.org/. (Accessed 8 February 2021).
Soto-Centeno, J.A., Steadman, D.W., 2015. Fossils reject climate change as the cause of extinction of Caribbean bats. Sci. Rep. 5, 7971. https://doi.org/10.1038/srep07971.
Sreekar, R., Huang, G., Zhao, J.-B., Pasion, B.O., Yasuda, M., Zhang, K., Peabotuwage, I., Wang, X., Quan, R.-C., Ferry Slik, J.W., Corlett, R.T., Goodale, E., Harrison, R.D., 2015. The use of species–area relationships to partition the effects of hunting and deforestation on bird extirpations in a fragmented landscape. Divers. Distrib. 21, 441–450. https://doi.org/10.1111/ddi.12292.
Sritongchuay, T., Kremen, C., Bumrungsri, S., 2016. Effects of forest and cave proximity on fruit set of tree crops in tropical orchards in southern Thailand. J. Trop. Ecol. 32, 269–279. https://doi.org/10.1017/S0266467416000353.
Stoner, K.E., Vulinec, K., Wright, S.J., Peres, C.A., 2007. Hunting and plant community dynamics in tropical forests: a synthesis and future directions. Biotropica 39, 385–392. https://doi.org/10.1111/j.1744-7429.2007.00291.x.
Tackett, E.S., Kingston, T., Sadeghmoghaddam, N., Rutrough, A.L., 2022. Global medicinal use of bats: a systematic literature and social media review. Diversity 14, 179. https://doi.org/10.3390/d14030179.
Tanalgo, K., Teves, R., Salvaña, F.R., Baleva, R., Tabora, John Aries, 2016. Human-bat interactions in caves of south central Mindanao, Philippines. Wildlife Biology in Practice 12, 1–14. https://doi.org/10.2461/wbp.2016.12.2.
Tanalgo, K.C., 2017. Wildlife hunting by indigenous people in a Philippine protected area: a perspective from Mt. Apo National Park, Mindanao Island. J. Threat. Taxa 9, 10307–10313. https://doi.org/10.11609/jott.2967.9.6.10307-10313.
Tanalgo, K.C., Hughes, A., 2021. The potential of bat-watching tourism in raising public awareness towards bat conservation in the Philippines. Environ. Challenges 4, 100140. https://doi.org/10.1016/j.envc.2021.100140.
Tanalgo, K.C., Hughes, A.C., 2019. Priority-setting for philippine bats using practical approach to guide effective species conservation and policy-making in the anthropocene. Hystrix It. J. Mamm. 30, 74–83. https://doi.org/10.4404/hystrix-00172-2019.
Tanalgo, K.C., Hughes, A.C., 2018. Bats of the Philippine islands—a review of research directions and relevance to national-level priorities and targets. Mamm. Biol. 91, 46–56. https://doi.org/10.1016/j.mambio.2018.03.005.
Tanalgo, K.C., Oliveira, H.F.M., Hughes, A.C., 2022. Mapping global conservation priorities and habitat vulnerabilities for cave-dwelling bats in a changing world. Sci. Total Environ. 843, 156909 https://doi.org/10.1016/j.scitotenv.2022.156909.
Tanalgo, K.C., Tabora, J.A.G., Hughes, A.C., 2018. Bat cave vulnerability index (BCVI): a holistic rapid assessment tool to identify priorities for effective cave conservation in the tropics. Ecol. Indic. 89, 852–860. https://doi.org/10.1016/j.ecolind.2017.11.064.
The Jamovi Project, 2020. Jamovi (Version 1.2). Computer Software.
The World Bank, 2022. GNI per capita, PPP (current international $) - East Asia & Pacific | Data [WWW Document]. https://data.worldbank.org/indicator/NY.GNP.PCAP.PP.CD?locations=Z4&name_desc=false accessed 7.28.22.
Trull, N., Böhm, M., Carr, J., 2018. Patterns and biases of climate change threats in the IUCN Red List. Conserv. Biol. 32, 135–147. https://doi.org/10.1111/cobi.13022.
Tulloch, V.J., Tulloch, A.I., Visconti, P., Halpern, B.S., Watson, J.E., Evans, M.C., Auerbach, N.A., Barnes, M., Beger, M., Chadès, I., Giakoumi, S., McDonald-Madden, E., Murray, N.J., Ringma, J., Possingham, H.P., 2015. Why do we map threats? Linking threat mapping with actions to make better conservation decisions. Front. Ecol. Environ. 13, 91–99. https://doi.org/10.1890/140022.
van Velden, J.L., Wilson, K., Lindsey, P.A., McCallum, H., Moyo, B.H.Z., Biggs, D., 2020. Bushmeat hunting and consumption is a pervasive issue in African savannahs: insights from four protected areas in Malawi. Biodivers. Conserv. 29, 1443–1464. https://doi.org/10.1007/s10531-020-01944-4.
Vincenot, C.E., Florens, F.B.V., Kingston, T., 2017. Can we protect island flying foxes? Science 355, 1368–1370. https://doi.org/10.1126/science.aam7582.
Wang, F., Winkler, J., Viña, A., McShea, W.J., Li, S., Connor, T., Zhao, Z., Wang, D., Yang, H., Tang, Y., Zhang, J., Liu, J., 2021. The hidden risk of using umbrella species as conservation surrogates: a spatio-temporal approach. Biol. Conserv. 253, 108913 https://doi.org/10.1016/j.biocon.2020.108913.
Welch, J.N., Beaulieu, J.M., 2018. Predicting extinction risk for data deficient bats. Diversity 10, 63. https://doi.org/10.3390/d10030063.
White, R.J., Razgour, O., 2020. Emerging zoonotic diseases originating in mammals: a systematic review of effects of anthropogenic land-use change. Mammal Rev. 50, 336–352. https://doi.org/10.1111/mam.12201.
Wiles, G., Brooke, A., 2009. Conservation threats to bats in the tropical Pacific islands and insular Southeast Asia. In: Island Bats: Evolution, Ecology, and Conservation, pp. 405–459.
World Bank database, 2022. Livestock production index (2014–2016 = 100) | Data [WWW Document]. https://data.worldbank.org/indicator/AG.PRD.LVSK.XD accessed 12.25.22.
Zhou, H., Chen, X., Hu, T., Li, J., Song, H., Liu, Y., Wang, P., Liu, D., Yang, J., Holmes, E. C., Hughes, A.C., Bi, Y., Shi, W., 2020. A novel bat coronavirus closely related to

SARS-CoV-2 contains natural insertions at the S1/S2 cleavage site of the spike protein. Curr. Biol. 30, 2196–2203. https://doi.org/10.1016/j.cub.2020.05.023 e3.
Zhou, H., Ji, J., Chen, X., Bi, Y., Li, J., Wang, Q., Hu, T., Song, H., Zhao, R., Chen, Y., Cui, M., Zhang, Y., Hughes, A.C., Holmes, E.C., Shi, W., 2021. Identification of novel bat coronaviruses sheds light on the evolutionary origins of SARS-CoV-2 and related viruses. Cell 184, 4380–4391. https://doi.org/10.1016/j.cell.2021.06.008 e14.
Zyambo, P., Kalaba, F.K., Nyirenda, V.R., Mwitwa, J., 2022. Conceptualising drivers of illegal hunting by local hunters living in or adjacent to African protected areas: a scoping review. Sustainability 14, 11204. https://doi.org/10.3390/su141811204.