REVIEW ARTICLES
ОБЗОРНЫЕ СТАТЬИ

WILL FUTURE EXTINCTIONS OCCUR AT THE SAME PLACES WHERE THE PAST ONES DID? A REVIEW INVOLVING MAMMALS AND THE IUCN RED LIST

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Eighty-five mammal species are classified worldwide as Extinct on the IUCN Red List. In this study, we aimed to assess to which Orders these species belong, when they became extinct and the factors that led to their extinction. We also compared the factors that threatened the survival of these species with the ones that are currently threatening the species classified as Critically Endangered, as well as the areas where the extinct species could be originally found with the areas where Critically Endangered species are currently found. Our review was conducted using the advanced search tool of the IUCN Red List database (Taxonomy, Red List Category, Threats and Land Regions filters). Rodentia was the mammal Order with the highest number of Extinct species, whereas Primates was the Order with the greatest proportion of Critically Endangered ones. The last two (19th and 20th) centuries were the periods in which the greatest number of species was lost. We found remarkable differences between the factors threatening species survival and between countries with the highest number of Extinct species and the ones that contain a greater number of Critically Endangered species. The threat category responsible for most of the extinctions overall was «Invasive and other problematic species, genes and diseases». Nonetheless, factors associated with habitat loss and degradation seem to have become more important nowadays and, in addition, some «new» factors, such as «Energy production and mining», «Human intrusions and disturbance», «Pollution», and «Transportation and service corridors», which have not had much relevance for past extinctions, now appear as important threats to Critically Endangered species. Australia was the country that has lost the most mammal species (n = 26), followed by Haiti (n = 9), the Dominican Republic (n = 8), and Cuba (n = 6). On the other hand, when we evaluated the amount of species classified as Critically Endangered, Madagascar (n = 33), Mexico (n = 27), and Indonesia (n = 26) are the countries that concentrate the highest number of them. Thus, future extinctions are unlikely to occur in the same places as in the past because the human society's relationship with the environment has changed over time: human population has grown, habitat loss has become the predominant threat to many species and new threat factors have emerged.

Key words: endangered species, extinct species, Mammalia, threat, threatened species

Introduction

Current animal extinction rates are much higher than those that have occurred during pre-civilization times, with some authors having estimated that wildlife is facing extinction rates 100 to 1000 times faster and more intensely than before (Pimm et al., 1995, 2014; Ceballos et al., 2015). It has even been considered that we are possibly witnessing a sixth mass extinction (Barnosky et al., 2011; Ceballos et al., 2015). According to Cho (2019), the extinction of species can have a series of consequences, such as causing cascading effects along the food chain (impacting other species and the ecosystem itself) and influencing the transmission of diseases, the occurrence of wildfires, the populational decline of some species with its increase of others (including invasive ones). Extinctions can also impact the livelihoods of people around the world and negatively affect ecosystem services, such as pollination and soil fertilisation (Cho, 2019).

Nearly 800 animal species are currently classified as Extinct (EX) according to the International Union for the Conservation of Nature (IUCN) Red List, with Chordata (n = 390), Mollusca (n = 299) and Arthropoda (n = 81) being the phyla with the largest number of Extinct species (IUCN, 2022). Within the phylum Chordata, the classes with most species classified as Extinct are Aves (birds, n = 159), Mammalia (mammals, n = 85) and Actinopterygii (ray-finned bony fishes, n = 78) (IUCN, 2022). Mammals, in particular, represent one of the best-studied groups of vertebrates, and most of the currently known species have had their conservation status assessed by IUCN. Additionally, they are also one of the most threatened animal groups, both in terms of the number of imperiled species and in terms of population losses (Ceballos & Ehrlich, 2002). Unsurprisingly, mammals have often been the focus of recent studies attempting to identify geographical patterns of spe-

cies extinctions. For instance, Loehle & Eschenbach (2012) demonstrated that terrestrial mammal extinctions have occurred at a much higher rate on islands than on mainland areas. Other studies, such as that of Davidson et al. (2017), have sought to uncover geographical correlates of mammal extinction risks based on both intrinsic and extrinsic traits of species, but did not discriminate between different IUCN threat status categories in their analyses, classifying taxa dichotomically as «at risk» and «not at risk». When we consider animal species that are facing an extremely high risk of extinction in the wild (i.e. species classified as Critically Endangered by the IUCN), we observe that 229 are mammals (IUCN, 2022). Nonetheless, the main factors responsible for past extinctions may be different from those that threaten species today and the areas where the Critically Endangered species are currently found may differ from the areas that have lost the most species in the past. However, we believe that understanding such patterns is essential to prevent further extinctions from occurring.

Since many of the mammal species currently classified as Extinct have been well studied and a considerable amount of information regarding their biology and ecology is known, mammals seem to be one of the animal groups most suitable for analyses comparing Extinct and threatened species. Herein, we aim to review the species that have become Extinct within the last six centuries, focusing on when they became Extinct, the threats that led to their extinction, and where these species could be found before going Extinct. We also aim to compare the threats that led these species to extinction with the ones that are currently threatening the species considered at greatest risk of becoming Extinct (i.e. Critically Endangered species, according to the IUCN), as well as compare the areas where those Extinct species could be originally found with the areas where the Critically Endangered species are currently found. Specifically, we tried to answer the following questions: Which groups (Orders) of mammals were most affected by extinction and in which of these groups are the Critically Endangered species classified? When did the extinction take place? Have most of the species gone Extinct recently or a long time ago? What led the species to extinction? What factors are threatening a larger number of species today? Which countries/areas/regions have lost the highest number of species? Are the areas that lost the highest number of species the same ones that are likely to lose more species in the near future? Given the biodiversity crisis scenario that we are currently facing, we hope to provide information that could eventually contribute to prevent future extinction.

Material and Methods

Our review was conducted using the advanced search tool of the IUCN Red List database (https://www.iucnredlist.org; IUCN, 2022) (accessed in 22.11.2021 and in 01.05.2022). Using the Taxonomy filter, we restricted our search to the Kingdom Animalia, then to the Phylum Chordata and, finally, to the Class Mammalia. Afterwards, using the Red List Category filter, we restricted our search to species classified under the Extinct (EX) conservation status. On each species' page, we searched for four specific types of information: the Order to which the species belonged, the year when the species were last seen, the factors responsible for their extinction (following the classification adopted by the IUCN: Agriculture and aquaculture; Biological resource use; Climate change and severe weather; Energy production and mining; Geological events; Human intrusions and disturbance; Invasive and other problematic species, genes and diseases; Natural system modifications; Pollution; Residential and commercial development; Transportation and service corridors), and the countries/regions where the species lived before disappearing. We compiled a large database with the information obtained (Table S1). However, we point out that IUCN only assesses, in the case of Extinct species, those that became Extinct after 1500. Many mammal species, including classical megafauna, became Extinct before that, and, therefore, they were not included in our database.

To obtain information about the Critically Endangered species, we performed a similar search. We used the same filters as in the previous step, but, rather than species classified as Extinct, we restricted our search to species classified under the Critically Endangered filter. However, this time, as our sole objective was to compare information (and not review the available information), we did not access the pages for each species. Thus, we only assessed the number of species that are threatened by each factor (in the Threats filter) and the number of species from each country/region (in the Land Regions filter). Finally, the results were analysed and compared from an exploratory perspective. We also tested whether the numbers of mammal species classified as Critically Endangered (CR) and as Extinct (EX) in each country are significantly correlated using Spearman rank

correlation using the STATISTICA v. 13.3 software (TIBCO Software Inc., USA).

Results

The 85 mammal species considered Extinct according to the IUCN belong to 12 Orders. The Order with the highest number of Extinct species was Rodentia (n = 38), followed by Chiroptera (n = 9), Cetartiodactyla (n = 8), Diprotodontia (n = 8) and Eulipotyphla (n = 7) (Fig. 1). The 229 mammal species classified as Critically Endangered belong to 15 Orders. The Orders with the highest number of species in this category were Primates (n = 86), Rodentia (n = 59), Chiroptera (n = 23), Cetartiodactyla (n = 15), Diprotodontia (n = 15) and Eulipotyphla (n = 11) (Fig. 1).

Considering the period when these extinctions occurred, we noted that, of the 59 species, for which the year they were last seen is known, 26 ones were last seen in the 20th century and 24 in the 19th century (Fig. 2). Only two species were last seen in the 21st century (not in Fig. 2, because the 21st century is not over yet).

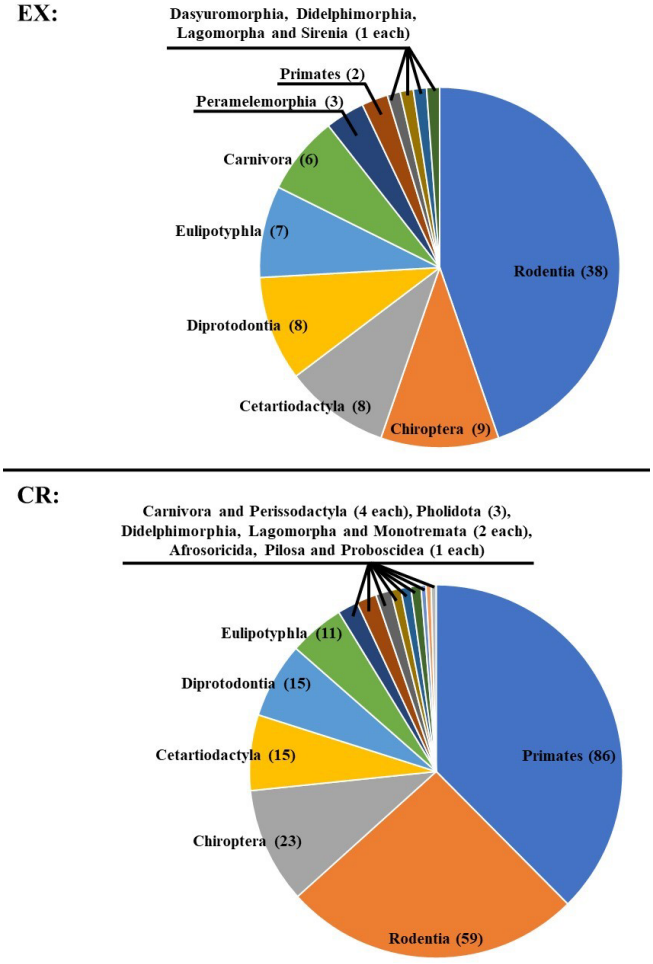

Fig. 1. Mammalian Orders and their numbers of Extinct (EX) and Critically Endangered (CR) species (number of species in parentheses).

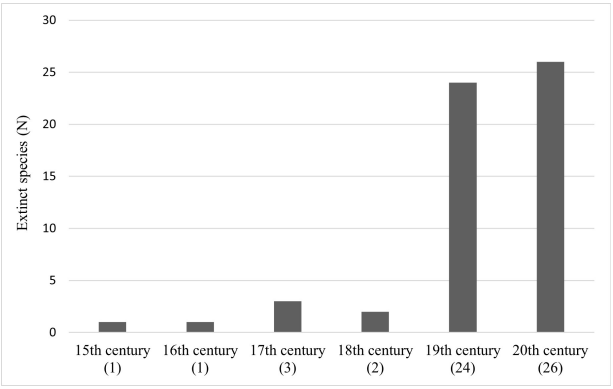

Fig. 2. Number (in parentheses) of mammal species that became Extinct in each century.

The threat category responsible for the extinction of most species was «Invasive and other problematic species, genes and diseases» (n = 40), followed by «Agriculture and aquaculture» (n = 22) and «Biological resource use» (n = 19). However, for 29 species the cause of extinction is unknown (Table 1). On the other hand, the factors threatening the survival of most Critically Endangered mammals were «Biological resource use» (n = 174), «Agriculture and aquaculture» (n = 166) and «Residential and commercial development» (n = 73) (Table 1).

Finally, considering the countries where those Extinct species occurred, Australia lost the highest number of mammal species (n = 26), followed by Haiti (n = 9), the Dominican Republic (n = 8), and Cuba (n = 6) (Fig. 3). Nonetheless, when we evaluated the number of species classified as Critically Endangered, Madagascar (n = 33), Mexico (n = 27), and Indonesia (n = 26) are the countries that occupy the first positions in the ranking (Fig. 3). There was a negative and significant correlation between the number of Extinct species and the number of Critically Endangered species per country (Spearman Rank Correlation: $\rho = -0.277$; $p < 0.001$).

Table 1. Number of mammal species that were/are threatened by each Threat factor according to IUCN classification

Threat	Extinct species	Critically Endangered species
Agriculture and aquaculture	22	166
Biological resource use	19	174
Climate change and severe weather	4	41
Energy production and mining	0	42
Geological events	1	7
Human intrusions and disturbance	0	31
Invasive and other problematic species, genes and diseases	40	52
Natural system modifications	7	59
Pollution	0	9
Residential and commercial development	1	73
Transportation and service corridors	0	36
Unknown	29	0

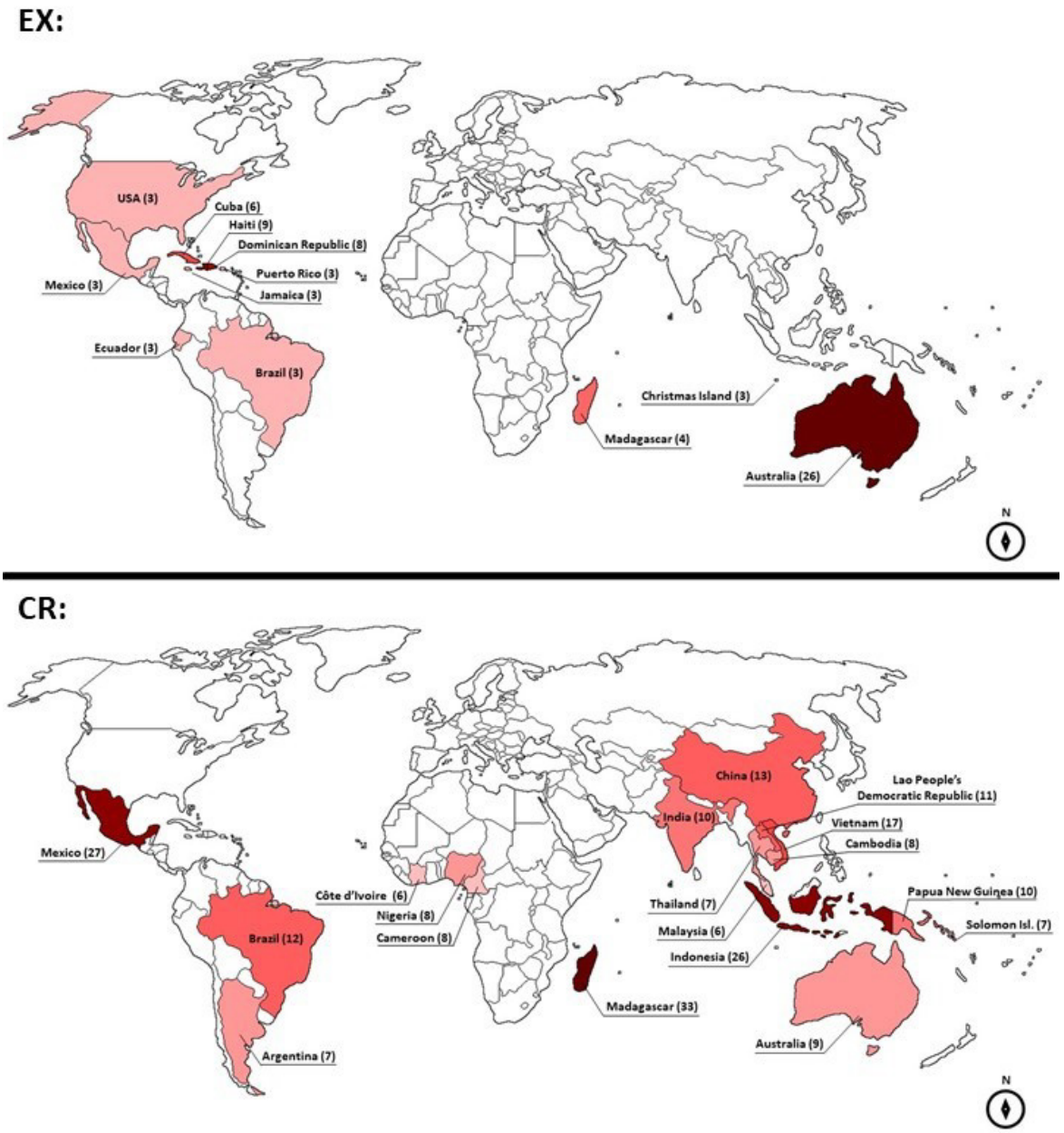

Fig. 3. Number of mammal species classified as Extinct (EX) and Critically Endangered (CR) per each country. To facilitate visualisation, countries with two or fewer Extinct species and countries with five or fewer Critically Endangered species are not highlighted. For the complete list of countries and their respective numbers of Extinct and Critically Endangered species see Table S2.

Discussion

A large portion of our Extinct mammal database is made up of small-bodied species (see Fig. 4). Regarding the mammal Orders that present a higher number of Extinct species, it can be observed that many of them, in fact, contain mainly small-bodied taxa. In this context, it is worth highlighting that body size is one of the most well studied traits related to extinction risk (Chichorro et al., 2019). There seems to be a consensus that large-bodied species are more susceptible to extinction risks when compared to small-bodied ones, as the former commonly present many characteristics that increase their susceptibility to extinction (McKinney, 1997), such as slow life-histories and a low population density (Purvis et al., 2000). Additionally, it is also believed that large-bodied species are more likely to be targeted by recreational hunting, when compared to smaller species (Cardillo, 2003). However, this could not be observed in our study, since most of the species that are already Extinct were small. This may simply reflect the fact that the vast majority of mammals are small-bodied and, therefore, the number of small Extinct species will tend to be greater than the number of large Extinct species regardless of how susceptible to extinction each indi-

vidual species is. Indeed, Rodentia and Chiroptera, the two mammal Orders with the highest total number of species and that contain mostly small-bodied representatives, were the Orders with the highest numbers of Extinct species. However, we did not expect that the ranking of the Orders with the Extinct species would be so similar to the ranking of the Orders with the Critically Endangered species. Despite the Order Primates having occupied the first position in the ranking of Critically Endangered species (and not being among the six Orders with the greatest number of Extinct taxa), the five subsequent Orders remained all in the same sequence: Rodentia > Chiroptera > Cetartiodactyla > Diprotodontia > Eulipotyphla. Habitat destruction and biological resource use are the most significant threat to primate populations (IUCN, 2022). These animals are threatened by several activities such as hunting for bush-meat, illegal trade as pets and body parts, climate change and diseases (Estrada et al., 2017).

Over the past few centuries, there seems to have been a marked increase in the number of Extinct mammals. As we have said, most species currently classified as Extinct (among those, for which year it was last seen is known) have become Extinct within the last two (i.e. 19th and 20th) centuries. Extinction rates rose from seven species by the late 18th century to 24 species that were last seen in the 19th century and 26 species in the 20th century. However, contrary to what we expected, only two species have become Extinct in the 21st century so far. They are *Melomys rubicola* Thomas, 1924 (Order Rodentia), and *Pipistrellus murrayi* Andrews, 1900 (Order Chiroptera). Coincidentally, both of them were last seen in the same year, in 2009. It is presumed that the *M. rubicola* population declined due to storm surges across its entire geographic distribution in Bramble Cay (Australia), and/or to ongoing and episodic reduction in vegetation, probably caused by the storm surges as well (Woinarski et al., 2014; Woinarski & Burbidge, 2016). The reasons for the decline of *P. murrayi* are unclear, although some believe that the species was affected by habitat loss and environmental changes, as well as by predation or disturbance caused by introduced species (Lumsden et al., 2017).

The factor responsible for the extinction of most of the species was «Invasive and other problematic species, genes and diseases». European colonisation appears to have been a determining factor in some of these extinctions, as it was the cause of some of the most famous introductions of exotic species (IUCN, 2022). The extinction of *Isolobodon portoricensis* Allen, 1916 (Order Rodentia), is a good example. The species, formerly found in the Dominican Republic and Haiti, became Extinct in the 16th century. It is believed that one of the main threats that led to this species' decline was predation by introduced mongooses and house rats (Turvey & Dávalos, 2018). Feral cats seem to have been responsible for the extinction of many species as well, such as *Notomys macrotis* Thomas, 1921 (Order Rodentia), a species endemic to Australia, which disappeared during the mid-19th century (Burbidge & Woinarski, 2016). In addition to rats, mongooses, and feral cats, we can mention dogs, foxes, cattle, and many other alien species as being responsible for native mammal extinctions worldwide. In some cases, the reason for the decline of species that are currently Extinct was not a competition with alien species or their predation by them, but other factors such as transmission of diseases and hybridisation (IUCN, 2022).

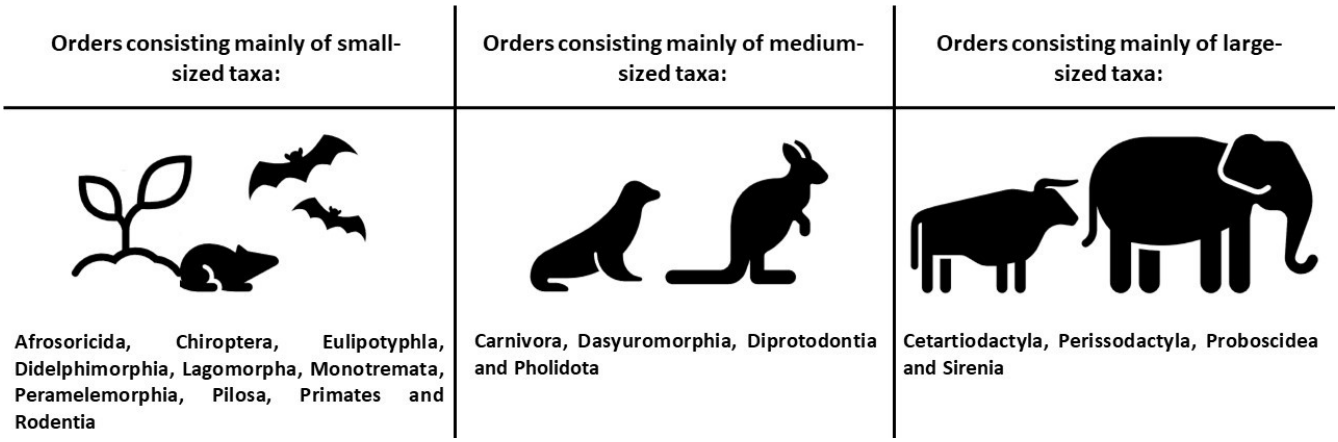

Fig. 4. Mammalian Orders (both Extinct and Critically Endangered) classified according to body size.

In turn, when we evaluate the factors that are currently threatening a higher number of Critically Endangered species, we notice that, while «Invasive and other problematic species, genes and diseases» has lost some prominence, the factors associated with habitat loss and degradation (including «Agriculture and aquaculture» and «Residential and commercial development») seem to have become more important. However, «Biological resource use» (n = 174) continues to be one of the most prominent factors. In addition, some «new» factors, which did not have much relevance for past extinctions, have nowadays appeared as important threats to Critically Endangered species. Such factors are: «Energy production and mining», «Human intrusions and disturbance», «Pollution», «Transportation and service corridors» and «Climate change and severe weather». We believe that such dissimilarities between the factors responsible for extinction in the past and factors, which are currently threatening Critically Endangered species not only reflect the way our society has developed over time (i.e. not only has human population increased in size, but is also interfering more intensely with the environment), but may also explain why future extinctions are unlikely to occur at the same places as in the past.

A comparison of the maps in Fig. 3 shows that most of the countries/regions that concentrate the highest number of Extinct mammal species are located at tropical latitudes, which is not surprising, considering that most of the world's biodiversity is found in the tropics. Nonetheless, we have also observed that many of those countries/regions are islands (see Table S2). In this context, it is noteworthy that many Caribbean islands were on the top of the list of countries with the highest number of Extinct mammals. Island extinction rates, in fact, tend to be higher than continental rates mainly because of the greater impact of factors such as introductions of alien predators and diseases (Loehle & Eschenbach, 2012). It is not surprising, thus, that many species have been extirpated from the Caribbean region. Nevertheless, Australia appears to have been the epicenter of mammalian extinctions. According to Woinarski et al. (2015), in contrary to other regions, where the main causes of extinction are habitat loss, hunting, and diverse impacts caused by human development, the loss of Australian terrestrial mammals was caused mainly by predation by introduced species and by changes in fire regimes. A similar pattern could be observed in our analysis, which showed that most of the Extinct mammals that could be found in the country were extirpated by two threat categories: «Invasive and other problematic species, genes and diseases» and «Agriculture and aquaculture».

Surprisingly, when comparing the areas that lost the most species with the areas where the Critically Endangered species are concentrated, there is a marked disparity. Indeed, we found a significant negative correlation between the numbers of Extinct and Critically Endangered species. This seems to indicate that the areas likely to lose more species in the future may not be the same ones that lost the most species in the past. Although most of the countries/regions that concentrate the highest number of Critically Endangered mammal species are also located at tropical latitudes, like Madagascar, Mexico, and Indonesia, leading the new ranking. However, other countries, such as Vietnam, China, Brazil, and the Lao People's Democratic Republic, were also found to be a home to a large number of Critically Endangered mammals. The situation is quite worrying in some of these countries and may be particularly critical for certain mammal groups. For example, of the 108 lemur (Order Primates, Strepsirrhini) species evaluated by the IUCN, all endemic to Madagascar, 104 (i.e. 96.3%) ones are classified as threatened (i.e. Critically Endangered, Endangered, or Vulnerable). Lemurs have even been considered by some authors as the world's most endangered mammals (e.g. Schwitzer et al., 2014), and the main threats to those primates seem to be related to habitat loss, along with other factors such as collecting for the pet trade and climate change (Salmona et al., 2017; Vieilledent et al., 2018; IUCN, 2022).

Indonesia, Vietnam, and the Lao People's Democratic Republic, being all geographically located in Southeast Asia, in turn, are home to several Critically Endangered mammals that are popular with the general public (i.e. «flag species»), like *Pongo* spp., *Nomascus* spp., *Pseudoryx nghetinhensis* Dung, Giao, Chinh, Touc, Arctander & MacKinnon, 1993, *Rhinoceros sondaicus* Desmarest, 1822, *Dicerorhinus sumatrensis* (G. Fischer, 1814), *Manis javanica* Desmarest, 1822, and *Manis pentadactyla* Linnaeus, 1758. Southeast Asia is facing a sharp wildlife decline, mainly due to deforestation (to obtain palm oil, paper, wood, and other commodities) (Hance, 2019). Furthermore, both illegal wildlife trade for Chinese traditional medicine, bushmeat, and the pet market, and the human population growth represent serious threats to the local wildlife (Hance, 2019). Indeed, Southeast Asia is considered one of the world's most critical regions regarding mammal

extinction risks, due to a combination of extrinsic and intrinsic traits of species occurring over there (Davidson et al., 2017). China, while home to some of the aforementioned species, also houses the last populations of wild *Camelus ferus* Przewalski, 1878, and of *Saiga tatarica* (Linnaeus, 1766), among several other threatened mammals (Shuai et al., 2021). There, habitat loss and degradation caused by human activities such as mining and pollution, wildlife trade to supply the traditional Chinese medicine market, and climate change represent serious threats to biodiversity (IUCN, 2022).

In the Neotropical realm, Mexico is the country that houses the highest number of Critically Endangered mammals, including *Phocoena sinus* Norris & McFarland, 1958, and many species of rodents and shrews. Factors, like climate change, habitat destruction, wildlife trade and direct killing of individuals, are considered the most worrisome threats for Mexican mammals (Olivera, 2018). Finally, Brazil, as one of the countries with the richest mammal fauna (Quintela et al., 2020), is home to several species classified as Critically Endangered, such as *Brachyteles* spp. and other primates. According to the Brazilian Red Book of Threatened Species (ICMBio/MMA, 2018), agriculture and livestock, hunting, transportation, urban expansion, and energy production are the factors that threaten the survival of the greatest number of mammal species in that country.

All the countries mentioned above represent rich territories in terms of biodiversity, with Brazil, Indonesia, China, Mexico, and Madagascar being a part of the 17 megadiverse countries list (Mittermeier et al., 1997). Since these countries already concentrate such zoological richness, it would be expected that they also present a high number of threatened taxa. However, our numbers reinforce the responsibility of such countries regarding species conservation.

Kerr & Currie (1995) stated that both natural and anthropogenic factors are important in determining a species' risk of extinction. However, they highlighted that little work has been done to quantify the magnitude of anthropogenic influences on the extinction process. Contrary to our study, Kerr & Currie (1995) did not find a very clear relationship between species loss and habitat loss. Thus, we hope that our study will contribute to clarify this relationship. At the same time, Kerr & Currie (1995) found that various measures of anthropogenic influence, including human population density, per capita gross national product, and extent of Protected Areas per country were closely related to the extinction risk.

Conclusions

With this study, we hope to have answered (or at least contributed to answering) the questions we have proposed. Future extinctions are unlikely to occur at the same locations as in the past because, as already mentioned, human society's relationship with the environment has changed over time. Human population has grown, habitat loss has become the predominant threat to many species, and new threat factors have emerged. In face of the current biodiversity crisis scenario, the IUCN Red List functions as an essential tool for the conservation of species. Their criteria, intended to be applicable to all species except micro-organisms, have been widely used by conservation practitioners and scientists (Mace et al., 2008). The information present there can and should be used to test hypotheses, perform advanced research, and answer important questions in Conservation Biology. We believe it is necessary to not only encourage the use of such a tool, but also to disseminate the information contained therein. In this way, we hope the present study may serve as a stimulus for other similar works to be done.

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Supporting Information

The information on mammal species analysed in the present review paper (Electronic Supplement. Data on the number of Extinct and Critically Endangered mammals according to the IUCN Red List per country with additional information for Extinct taxa) may be found in the **Supporting Information**.

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БУДУТ ЛИ БУДУЩИЕ СЛУЧАИ ИСЧЕЗНОВЕНИЯ ВИДОВ ПРОИСХОДИТЬ ТАМ ЖЕ, ГДЕ И В ПРОШЛОМ? ОБЗОР МЛЕКОПИТАЮЩИХ И КРАСНОГО СПИСКА МСОП

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В Красном списке Международного союза охраны природы (МСОП) 85 видов млекопитающих классифицированы как вымершие (Extinct, EX). В этом исследовании мы стремились оценить, к каким отрядам принадлежат эти виды, когда они вымерли и какие факторы привели к их исчезновению. Мы также сравнили факторы, которые угрожали этим видам, с теми факторами, которые в настоящее время угрожают видам, классифицированным в Красном списке МСОП как находящиеся на грани исчезновения (Critically Endangered, CR). Также изучили регионы, где вымершие виды могли изначально встречаться, с регионами, где в настоящее время встречаются виды, находящиеся на грани исчезновения. Наш обзор был проведен с использованием инструмента расширенного поиска в базе данных Красного списка МСОП (с фильтрами «Таксономия», «Категория Красного списка», «Угрозы» и «Регионы суши»). Грызуны (Rodentia) были отрядом млекопитающих с наибольшим количеством вымерших видов, тогда как приматы (Primates) были отрядом с наибольшей долей видов, находящихся под угрозой исчезновения. XIX–XX вв. были периодами исчезновения наибольшего числа видов млекопитающих. Мы обнаружили заметные различия между факторами, угрожающими выживанию видов, и между странами с наибольшим числом вымерших видов и странами, в которых проживает наибольшее количество видов, находящихся на грани исчезновения. Категория угрозы, ставшая причиной наибольшего числа исчезновений видов млекопитающих в целом, была «Инвазивные и другие проблемные виды, гены и болезни». Тем не менее, факторы, связанные с уничтожением и нарушением среды обитания, в настоящее время, по-видимому, стали более важными. Кроме того, некоторые «новые» факторы («Производство и добыча энергии», «Человеческое влияние и беспокойство с его стороны», «Загрязнение» и «Транспорт и служебные коридоры»), которые не имели большого значения для исчезновений видов в прошлом, теперь представляют собой серьезную угрозу для видов, находящихся на грани исчезновения. Австралия была страной, которая потеряла наибольшее количество видов млекопитающих (n = 26); за ней следуют Гаити (n = 9), Доминиканская Республика (n = 8) и Куба (n = 6). С другой стороны, когда мы оценили количество видов, отнесенных к категории находящихся под угрозой исчезновения, Мадагаскар (n = 33), Мексика (n = 27) и Индонезия (n = 26) были странами, в которых сосредоточено их наибольшее количество. Таким образом, маловероятно, что будущие исчезновения видов произойдут в тех же местах, что и в прошлом, потому что взаимодействие человечества с окружающей средой с течением времени изменилось: население человечества выросло, а утрата среды обитания стала преобладающей угрозой для многих видов, а также появились новые факторы угрозы.

Ключевые слова: Mammalia, вид под угрозой исчезновения, исчезнувший вид, угроза, уязвимый вид