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REVIEW

A global review of the conservation threats and status of mustelids

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ABSTRACT

1. The family Mustelidae is the largest among the order Carnivora. While we know a great deal about certain species, there is still a lack of information about many mustelids.
2. We first investigated the International Union for Conservation of Nature (IUCN) Red List species-level assessments for each mustelid species. Then, we undertook a systematic review of the scientific literature with the aim of identifying the primary threats and subthreats reported, and which species are most studied. Threats are defined by the IUCN as "the proximate human activities or processes that have impacted, are impacting, or may impact the status of the taxon".
3. We analysed 1003 published articles. For each article, we collected year of publication, geographical zone of each study, species studied, and the threats and subthreats identified.
4. The majority of species (62%) were classified as Least Concern on the IUCN Red List, but 31 out of 63 species were found to be declining globally and only two species were increasing. The species studied and location of studies were biased, with 72% of studies undertaken in North America or Europe and focussing on very few species. A high proportion of species distributed predominantly in the tropics were categorised as declining, and threats linked with hunting, fishing, and logging were identified as the most common for mustelids by the IUCN Red List and in the scientific literature. Differences in the proportion of threats affecting each subfamily were also reported.
5. The nature of threats varies in different parts of the world and between species. It is essential to undertake more research with a strong focus towards species in highly biodiverse regions. A greater understanding of threats such as wildlife pet trade, emerging diseases, and climate change must also be central to prevent declines.

INTRODUCTION

Many carnivores (here defined as Carnivora) have undergone substantial declines in their populations and geographical ranges around the world (Ripple et al. 2014). As predators, typically at or near the top of their food chains, carnivores play an important role in ecosystems (Ritchie et al. 2012). The Mustelidae is the largest and most diverse family within the order Carnivora, comprising 63 extant species as reported by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Mustelids vary greatly in size, lifestyles, and life-history traits, and have adapted to all types of climates and habitats throughout all continents, with the exception of Antarctica and Australasia. They often occupy regions with highly seasonal environments and have relatively large home ranges and therefore lower population densities than many other carnivores (Ferguson & Larivière 2005). Mustelids have had a long association with humans, and many species hold cultural or economic significance, with particular value as furbearers and in rodent (pest) control (Schreiber et al. 1989).

Some mustelids are highly vulnerable to impacts from anthropogenic activities and have already undergone numerical or distributional declines (Chanin & Jefferies 1978, Thompson 1991, Finch 1992, Ruggiero et al. 1994, Wilson et al. 2000). In the case of the sea mink *Neovison macrodon*, overhunting for fur led to its extinction by the late 19th century (Campbell 1988). The sea otter *Enhydra lutris* was also heavily hunted for fur in the 18th and 19th centuries. Local extinctions led to huge increases in numbers of sea urchins *Mesocentrotus franciscanus*, the main prey of *Enhydra lutris*, which in turn resulted in the loss of kelp (Laminariales) beds that the sea urchins consumed. After concerted conservation efforts, *Enhydra lutris* recovered in the second part of the 20th century.

Although we may know a great deal about the threats and risk of extinction of certain members of the mustelid family (Bright 2000), the naturally low densities, cryptic appearance, behaviour, and lack of study of others mean that little is known about many, particularly the smaller mustelids (Westra 2019). Therefore, there is a very real danger that some species could be in danger of extinction before it is realised. Increasing concern around certain mustelids (Croose et al. 2018, Coomber et al. 2021, Jachowski et al. 2021, Marneweck et al. 2021) makes the assessment of the conservation status and an analysis highlighting the major threats and knowledge gaps facing the Mustelidae family important.

In this study, we investigated the conservation status (IUCN category), population trends, and threats to mustelids as reported by the IUCN Red List of Threatened Species. Then, we conducted a systematic review of the mustelid-related scientific literature aiming to identify: (1) the primary threats and subthreats reported in the literature, (2) the regions where these threats are reported, and (3) which species and subfamilies are the most studied.

METHODS

Summary of the conservation status of mustelids

We first investigated the conservation category, population trends, and threats identified for each mustelid species reported by the IUCN Red List of Threatened Species (global assessment data and range data; IUCN 2020). Threats are listed by the IUCN and are defined as 'the proximate human activities or processes that have impacted, are impacting, or may impact the status of the taxon'. Then, we identified where most mustelid populations were declining based on their ranges and global population trends, and compared the proportion of mustelid species reported as Least Concern, Vulnerable, Near Threatened, Endangered, Critically Endangered and Data Deficient with the proportions of the 193 other non-pinniped Carnivora species from the IUCN Red List of Threatened Species.

Systematic review of the scientific literature

We used the Web of Science search engine to identify articles published from 1900 to 2020 (June) with the following search words: ("mustelid*" OR "Mustela" OR [followed by the genus of all other mustelid species]) AND ("conservation*" OR "threat*" OR "status*" OR "declin*" OR "recover*"). We also added articles on mustelids from the *Small Carnivore Conservation* journal, which is published by the *IUCN SSC Small Carnivore Specialist Group*, and the *IUCN SSC Otter Specialist Group (OSG) Bulletin*, which do not appear through the search engine.

We used a PRISMA framework (Moher et al. 2009, Shamseer et al. 2015) to define our inclusion criteria (Fig. 1). This framework provides multiple successive screening steps and treats selected publications equally. We excluded studies if no clear threats were identified in the title or abstract during the first screening process. Then, we assessed the full text for the remaining studies and inclusion criteria were reapplied. We retrieved the following information from each article: year of publication, country (or area), geographical zone (seven categories) of each study, whether threats were identified first-hand or reported from other studies, species, subfamily, and the threats and subthreats identified by using the IUCN Threats Classification Scheme (version 3.2; https://www.iucnredlist.org/resources/threat-classification-scheme). Each author participating in the systematic review verified 5% of articles that had gone through the screening process, selected by a random number generator, to ensure consistency throughout the review. Concerted decisions were taken if any inconsistencies were identified. We performed two-proportions z-tests with the R function *prop.test* (R Core Team 2021) to test for differences between the proportion of publications for each threat and subthreat in different subfamilies and differences between the proportion of threats identified by the IUCN Red List for different subfamilies.

RESULTS AND DISCUSSION

Conservation status of mustelids

We found that mustelid species richness was highest between eastern China and South-East Asia and in the higher

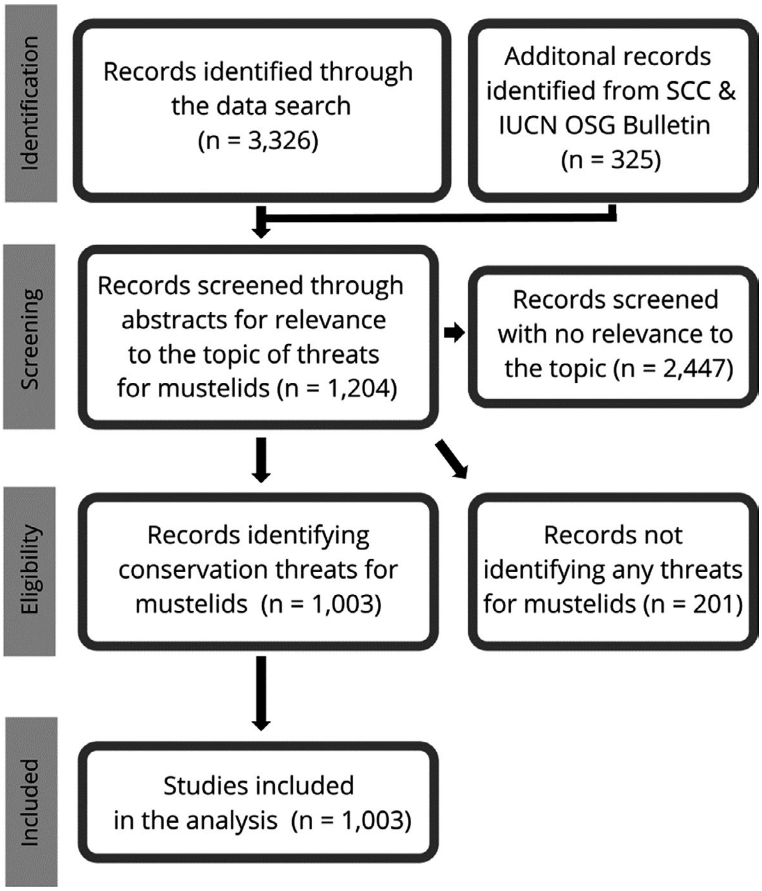

Fig. 1. PRISMA flow diagram showing the procedure followed in this study. SCC stands for the Small Carnivore Conservation journal, and the IUCN OSG stands for the Otter Specialist Group Bulletin.

latitudes of the Northern Hemisphere: over 10 species occur in parts of these areas (Fig. 2a). Mustelid species with a decreasing population trend were mostly distributed in the tropics – for example, up to 80% of species are declining in South-East Asia (Fig. 2c). The majority of mustelid species (39 species, 62%) were classified as Least Concern by the IUCN (Fig. 2b). Populations of 31 out of 63 species were found to be declining globally, 12 remained unknown, only two species were increasing, while other species were stable (Fig. 2d). For each conservation category, mustelid species represented approximately 25% of all non-pinniped carnivores, which is equivalent to the overall proportion of mustelids, with the exception of Data Deficient species, where mustelids represented half of non-pinniped carnivores (Fig. 3). The threats of 50 species were available, while 13 species, mostly in the Mustelinae subfamily, were assessed as facing no major threats, or as having insufficient knowledge to determine threats. Biological resource use (by humans) was the most prominent threat (76% of all mustelids are affected by this threat), followed by agriculture/aquaculture and residential development. Human disturbance, energy production/mining, and climate change were the least reported threats, with 11% of species known to be affected (Fig. 2e).

Systematic review

The Web of Science search combined with the mustelid literature from the *Small Carnivore Conservation* journal and the *IUCN SSC Otter Specialist Group Bulletin* identified 3651 articles. Following the PRISMA protocol, we excluded 2447 articles because they did not clearly identify any threats for the species of interest (Fig. 1). These articles were mostly linked with pathogen transmission to other species (e.g. *Meles meles* and bovine tuberculosis transmission to cattle) or the impact of invasive mustelid species (e.g. *Mustela erminea* in New Zealand). A total of 1003 articles were included in the final analysis, and 713 of these reported threats first-hand.

Geography

Articles identifying threats to mustelids were identified on all continents where mustelids are native, but 72% of the

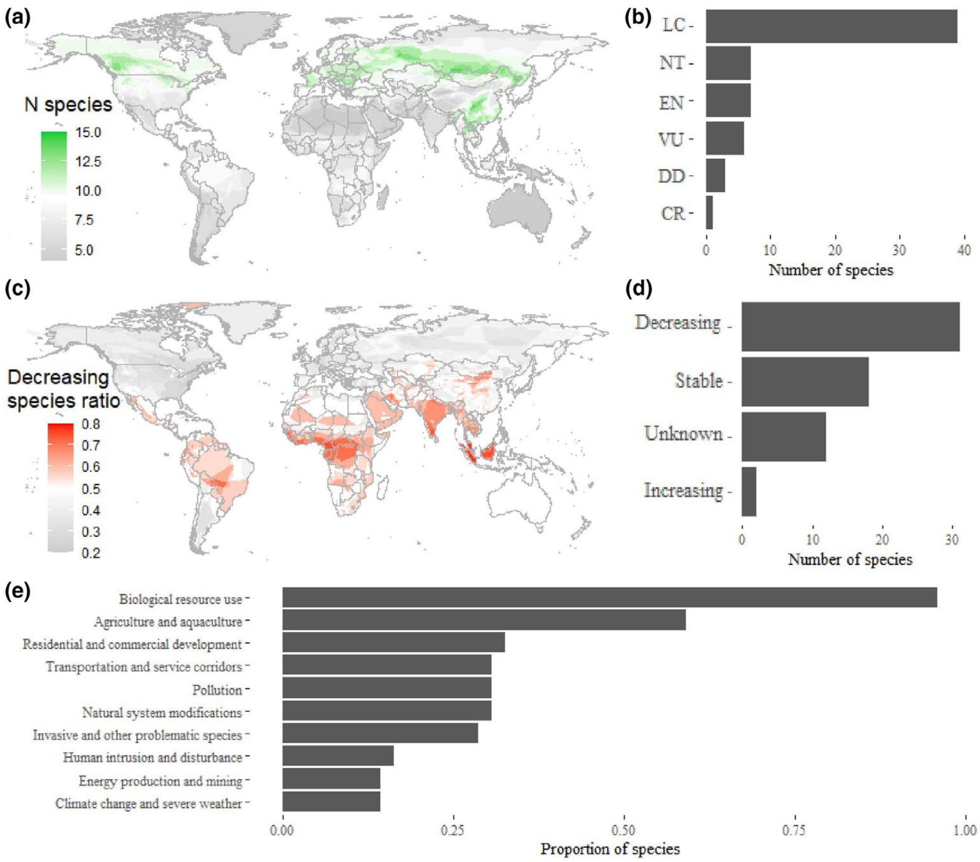

Fig. 2. Summary of information available for all 63 mustelid species from the IUCN Red List; (a) species richness throughout the world; (b) frequency of each IUCN conservation category; (c) ratio of decreasing species; (d) frequency of the population trends reported; and (e) proportion of species for which threats have been identified (50 species) affected by each threat according to the IUCN.

studies took place in North America (339) or in Europe and Central Asia (391; Fig. 4a). The USA was the country (or area) with the most articles identifying threats to mustelids (249), followed by an additional 16 areas mostly in Europe with 12 or more studies each, and 93 areas with fewer than 12 studies (40 areas with a single study; Fig. 4b).

The first articles included were published in the late 1970s; numbers strongly increased from 1990 onwards and may have plateaued between 2010 and 2019 with an average of 46.3 publications per year (Fig. 4c). This increase in the number of publications is likely to reflect the overall increase in the number of publications in most scientific fields (e.g. Greenville et al. 2017, Cartagena-Matos et al. 2021, Maas et al. 2021, Mas et al. 2021).

The breadth of scientific literature from Europe and North America reflects the general pattern that is found in most scientific research (e.g. Shannon et al. 2016, Jerem & Mathews 2020, Maas et al. 2021), owing to a higher capacity for research and more funding there than in the most biodiverse countries in tropical regions (i.e. more well-resourced NGOs, more universities; dos Santos et al. 2020). A considerable amount of conservation-related literature is available from the tropics (e.g. via the SAFE Project), but these papers are rarely focused on single species unless they are undertaken on large charismatic fauna. Mustelids have received very little attention, as many species happen to be challenging to study, may be considered as low conservation priority in these regions compared with other carnivores, and rarely benefit directly from funding (Mammola et al. 2020). No scientific literature was available for many tropical species, meaning that little is known about their ecology and there are still difficulties in identifying some species (e.g. *Melogale* sp.; Shepherd 2012). Nonetheless, forests, a key habitat for many species, in the tropics are disappearing at a faster rate than any other habitats (Fischer et al. 2020), and mustelid species either lack a special designated conservation category in these areas, or, where legal protection exists, incidences of persecution remain high.

The scientific literature identifying threats for mustelids is also largely biased towards very few species from the

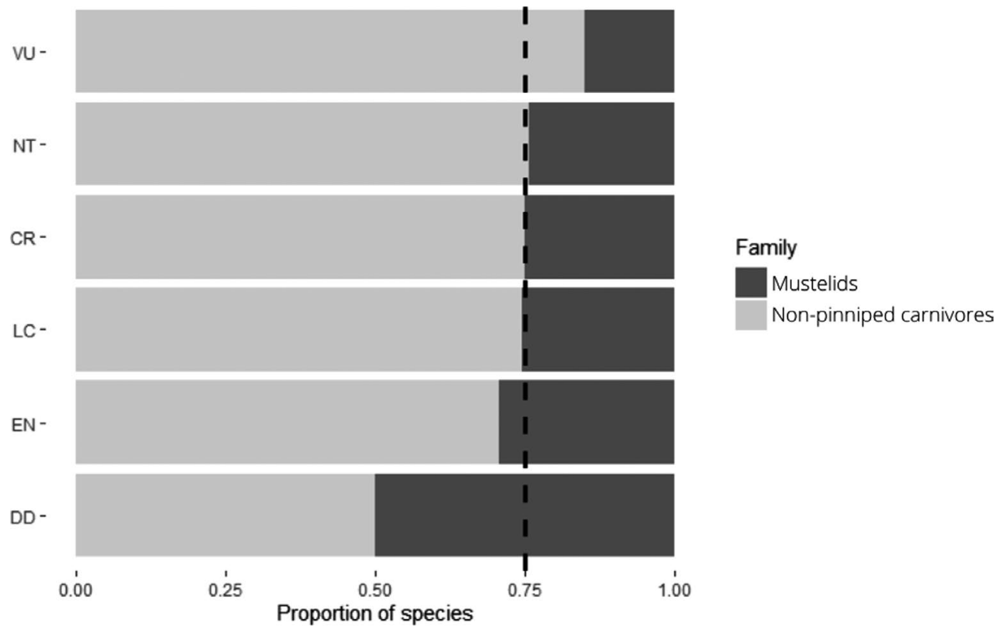

Fig. 3. Proportion of mustelids reported as Vulnerable (VU), Near Threatened (NT), Critically Endangered (CR), Least Concern (LC), Endangered (EN), and Data Deficient (DD) in comparison with non-pinniped carnivores. The dashed line represents the overall proportions of terrestrial carnivores that are non-pinnipeds (0.75) and mustelids (0.25). If mustelids extend to the left of the dashed line, a larger proportion of mustelid species has been reported for this category.

Northern Hemisphere, which have suffered population declines. For some of these species, the cause of decline has been straightforward to identify, which has resulted in an abundance of literature on a specific topic (see Lutrinae discussion). For example, the impact of oil spills on *Enhydra lutris* has regularly been studied, yet this threat almost exclusively affects this mustelid species. For tropical species, the number of threats remained relatively high, with biological resource use, which comprises a wide variety of subthreats (e.g. hunting, logging, conflict with fisheries), being the most recurrent threat. These findings also mirrored those identified in large carnivores by Ripple et al. (2014).

The *Small Carnivore Conservation* journal and *IUCN SSC Otter Specialist Group Bulletin* provided a significant proportion of articles on less-studied species, particularly those from the tropics, highlighting the importance of small specialist journals in disseminating essential information on single species. We did not include the ‘grey’ (unpublished) literature, and it is likely that additional resources are available from many other non-English-speaking countries.

Threats

In the scientific literature, threats were identified for 50 of the 63 (79%) extant mustelid species. These threats were mostly identified for species from three subfamilies: 37 species (74%) with threats were part of the Lutrinae, Guloninae, or Mustelinae subfamily (Fig. 5). In the scientific literature, we found significant differences in the proportion of publications reporting each threat between subfamilies (Fig. 6a; Appendix S1). In the IUCN Red List, we found significant differences in the proportion of species affected by each threat in each subfamily, with the exception of invasive and other problematic species, genes, and diseases (Fig. 6b; χ^2 = 5.8327, d.f. = 3, P = 0.12; Appendix S1). We identified subthreats for each threat and reported the proportions of publications reporting each subthreat for each subfamily (Fig. 7). With the exception of the impact of hunting and trapping, which was high for all subfamilies, we found significant differences in the proportion of publications reporting all subthreats between subfamilies (Fig. 7; Appendix S2), meaning that each subfamily was perceived as facing a different mix of threats and subthreats.

Lutrinae

For the Lutrinae subfamily, research has mostly taken place in the Northern Hemisphere and reflects where species richness is highest. Most threats identified in the literature affect very few species. *Lutra lutra* (225 papers; Fig. 5), *Enhydra lutris* (106), and *Lontra canadensis* (49) are perceived as charismatic species throughout most of their range and have undergone significant population declines

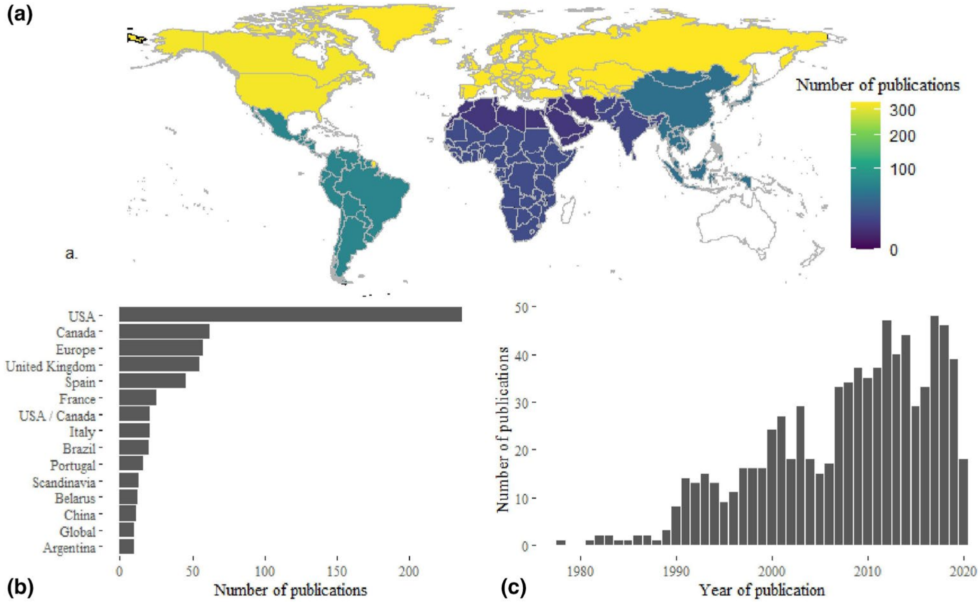

Fig. 4. Summary of published papers reporting threats for mustelid conservation; (a) distribution of the numbers of published papers reporting threats to mustelid conservation in seven geographical zones; (b) frequency of papers published in the 17 countries (or areas) with the most publications; and (c) number of publications between the late 1970s and 2020.

during the 19th and 20th centuries, followed by recoveries in parts of their range (e.g. *Lutra lutra* in Britain; Sainsbury et al. 2019). Being semi-aquatic, members of this subfamily are particularly sensitive to multiple forms of water pollution, and their dense fur meant that they were highly targeted during the peak of the fur trade, leading to their initial decline. The main pollutants leading to the decline of *Lontra canadensis* and *Lutra lutra* populations in the second part of the 20th century are polychlorinated biphenyls and organochlorine (Mason et al. 1992, Elliott et al. 2008), while *Enhydra lutris* has mostly been affected by oil spills (Garrott et al. 1993). These stochastic events, such as the Exxon Valdez oil spill in 1989, are thought to have resulted in the death of thousands of individuals (Garrott et al. 1993). Such declines and threats instigated most of the literature available on the Lutrinae subfamily to this day. Other species, which are mostly found in the tropics, have received very little attention. While pollution is likely to have an important impact on these species, the amount of literature available on the topic may overshadow other significant threats. Despite being represented in less literature, the diversity of threats reported for other Lutrinae species remains high. The construction of dams, along with conflicts with fisheries, transportation, urbanisation, human disturbance, and mining, is cited as important threats for these species (e.g. Ali et al. 2010, Charre-Medellín et al. 2011). The fur and skin trade is also currently prevalent, and increased exposure on social media has recently resulted in the emergence of wildlife pet trade as a new threat (Harrington et al. 2019), along with the risk posed by climate change for African species (Cianfrani et al. 2018).

Guloninae

The Guloninae subfamily, which comprises the genera *Martes*, *Pekania*, *Gulo*, and *Eira*, is mostly distributed in the Northern Hemisphere. While the literature is dominated by research on *Gulo gulo* (70 papers; Fig. 5), many studies have been undertaken on *Martes* and *Pekania* species in North America and Europe (136 papers). Biological resource use was the most commonly reported threat in the scientific literature. Most Guloninae species are highly valuable furbearers and have been the focus of intensive trapping for fur harvesting. This resulted in extensive historical declines for many species. Although some populations are recovering, most have yet to reach historical levels (Proulx et al. 2005). The partial recovery of some Guloninae species can be attributed to reductions in trapping pressure, due to either regulations on trapper harvests such as quota-based hunting (e.g. *Gulo gulo*, *Martes americana* and *Pekania pennanti*; Fawley 2019, Lansink et al. 2020) or full legal protection, resulting in trapping being prohibited (e.g. *Martes martes*; see https://www.nature.scot/professional-advice/protected-areas-and-species/protected-species/protected-species-z-guide/protected-species-pine-martens). Some species have also benefited from translocation and reintroduction programmes (e.g. *Pekania*

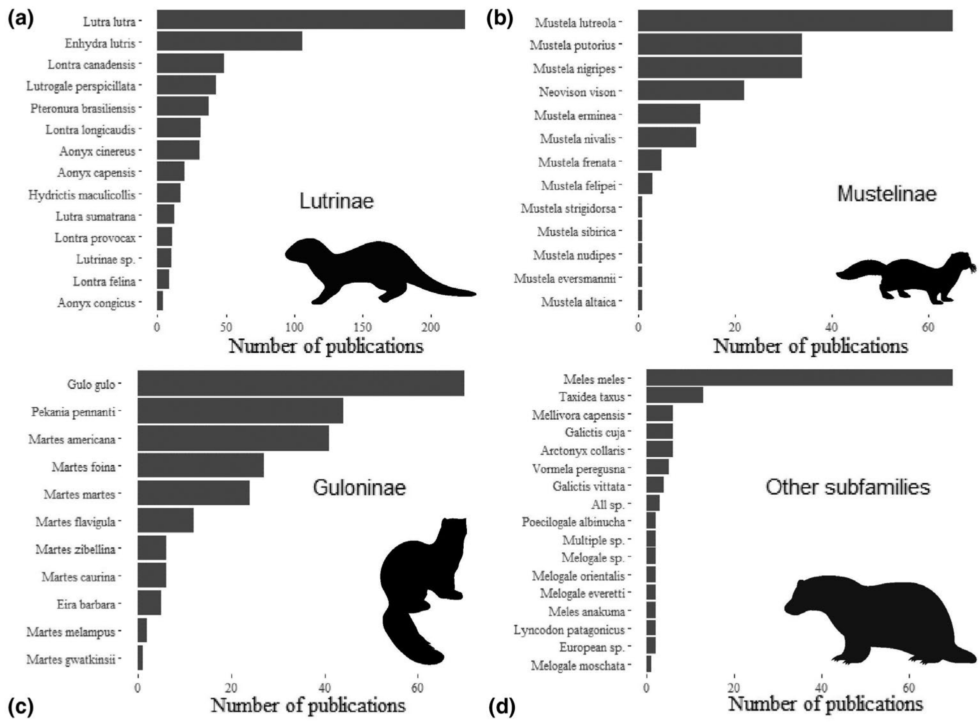

Fig. 5. Number of publications identifying threats for each species of (a) the Lutrinae subfamily; (b) the Mustelinae subfamily; (c) the Guloninae subfamily; and (d) other subfamilies.

pennanti, *Martes zibellina* and *Martes martes*; Lewis et al. 2012, Monakhov et al. 2018, McNicol et al. 2020). While the extent of the threat from trapping has almost certainly reduced over the last few decades, many of these species are still susceptible to overharvesting, because of their relatively low reproductive rates (Helldin 2000).

The threat of biological resource use also included the loss and alteration of woodland, through forestry practices such as logging. Guloninae species are mostly solitary, range over large areas, and are dependent on forested habitats. This makes them particularly vulnerable to forest fragmentation and degradation (Proulx et al. 2005). The impact of forest harvesting and management strategies has, consequently, been well studied for some species and remains an important threat (Hargis et al. 1999, Sidorovich et al. 2008, Mathai et al. 2017).

Although all mustelid subfamilies are impacted by transportation and residential development according to the IUCN, this threat was mainly identified in the scientific literature for Guloninae species, principally *Gulo gulo* (Dawson et al. 2010, May et al. 2012) and *Martes foina* (Grilo et al. 2012).

The impact of climate change has been more intensively studied for Guloninae species than for other subfamilies. *Gulo gulo* is particularly vulnerable to a warming climate and declining snowpack (Peacock 2011), and milder winters may increase the niche overlap between *Martes americana* and *Pekania pennanti*, favouring the last over the first (Suffice et al. 2017, Pauli et al. 2022). To a lesser extent, diseases in *Pekania pennanti* (Larkin et al. 2011) and *Martes foina* (Tavernier et al. 2012) have also received attention.

Mustelinae

Mustela lutreola (65 papers; Fig. 5) and *Mustela nigripes* (34) were two of the top three most reported species and have been the focus of extensive research effort, probably due to their rarity. *Mustela lutreola* is Critically Endangered (Maran et al. 2016), and *Mustela nigripes* is Endangered after having become extinct in the wild in the 1980s; it was subsequently reintroduced (Belant et al. 2015). Other more common species in the Northern Hemisphere, however, have received less attention in the scientific literature (e.g. *Mustela erminea* and *Mustela nivalis*), and there are still no efficient methods to monitor their populations at a broad scale.

Invasive and other problematic species, genes, and diseases were the most reported threat for the Mustelinae subfamily from the literature. This is likely to be due to the severity of these threats, particularly for endangered species. The threat from invasive species primarily comes

Fig. 6. (a) Proportion of publications identifying each threat in the scientific literature for each subfamily within the Mustelidae, and (b) the proportion of species in each subfamily that is assessed as being impacted by each threat according to the IUCN Red List (fitted scale)

from *Neovison vison*: it poses a significant threat to *Mustela lutreola* (Sidorovich et al. 1999, Põdra et al. 2013, Põdra & Gómez 2018) and, to a lesser extent, *Mustela putorius* (Melero et al. 2012, Barrientos 2015). Conversely, research has also targeted the effect of *Mustela nivalis* and *Mustela erminea* as invasive species in New Zealand (Cuthbert & Davis 2002), but these papers were not included in the analysis as these are threats posed by, not faced by, mustelids. A number of diseases and parasites have been reported to affect Mustelinae species. The sylvatic plague threatens the long-term recovery of *Mustela nigripes* populations (Biggins & Godbey 2003, Matchett et al. 2010), and Aleutian mink disease may be contributing to the population decline of *Mustela lutreola*, although further research to ascertain the impact is needed (Manas et al. 2001). Hybridisation has also been reported as a threat affecting *Mustela lutreola* (Lodé et al. 2005), *Mustela putorius* (Costa et al. 2013), and *Neovison vison* (Kidd et al. 2009), although the implications of this are often not widely understood.

Pollution was the second most reported threat for Mustelinae, and secondary exposure to anticoagulant rodenticides is seen as the main pollutant-related impact for Mustelinae. This has been reported in *Mustela putorius* (Sainsbury et al. 2018), *Mustela nivalis* and *Mustela erminea* (McDonald et al. 1998), and *Mustela lutreola* (Fournier-Chambrillon et al. 2004). Being semi-aquatic, like the Lutrinae subfamily, *Neovison vison* and *Mustela lutreola* are also threatened by water pollution (Giesy et al. 1994, Zabala et al. 2006).

Biological resource use was less commonly reported as a threat, because Mustelinae species tend to be less valued as furbearers than other subfamilies. While reported less than other threats, agriculture, reductions in prey availability, and transportation networks were also considered as threats to some species, such as *Mustela nigripes* (Miller & Reading 2012, Santymire et al. 2014).

There was no or very little information identified in our search for several species occurring in the tropics, such as *Mustela africana*, *Mustela lutreolina*, *Mustela altaica*, and *Mustela kathiah*. In the sparse literature available for species in the tropics, biological resource use, pollution, agriculture, residential development, and energy production have been reported as threats (e.g. *Mustela felipei*; Burneo

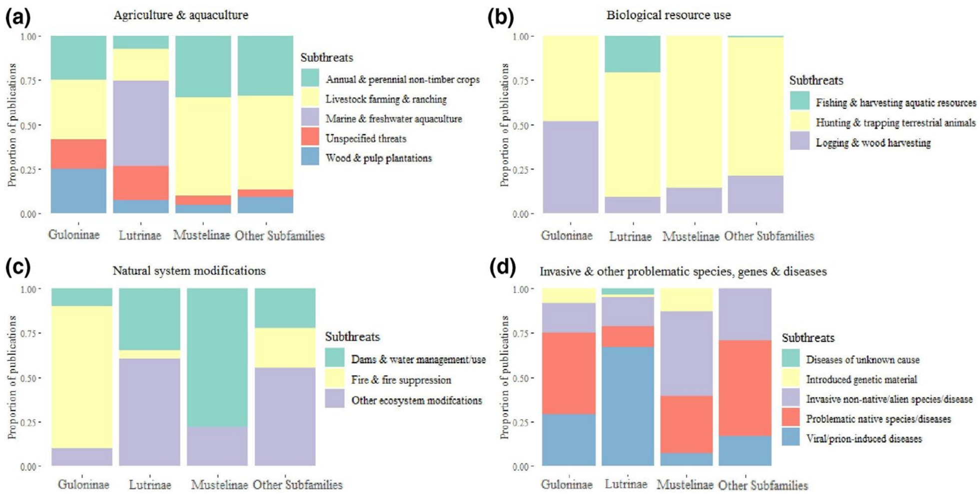

Fig. 7. Proportion of publications reporting each subthreat for each Mustelidae subfamily: (a) agriculture and aquaculture (χ^2 = 98.62, d.f. = 12, P < 0.001); (b) biological resource use (χ^2 = 115.12, d.f. = 6, P < 0.001); (c) natural system modifications (χ^2 = 82.30, d.f. = 6, P < 0.001); and (d) invasive and other problematic species, genes, and diseases (χ^2 = 104.35, d.f. = 12, P < 0.001).

et al. 2009). In addition, ten Mustelinae species were assessed as having no threats by the IUCN Red List, as some of the threats that may have been identified in the literature were thought to be not operating sufficiently widely or intensively to be relevant at the species level.

Other subfamilies

This group comprised the genera *Meles*, *Taxidea*, *Mellivora*, *Melogale*, *Arctonyx*, *Galictis*, *Vormela*, *Lyncodon*, and *Poecilogale*. With the exception of the two most commonly reported species, *Meles meles* (70 papers; Fig. 5) and *Taxidea taxus* (13), these mustelids are mostly found outside Europe and North America and in or closer to the tropics, where threats linked to biological resource use are prominent (e.g. poaching, legal harvesting, and deforestation). This trend was observed in the scientific literature and also showed similarities to the threats faced by Guloninae species. Mustelids from 'other subfamilies' are either impacted through direct persecution (e.g. *Meles meles*, *Taxidea taxus* and *Mellivora capensis*; Long 1992, Domingo-Roura et al. 2006, Turk Qashqaei et al. 2015), wildlife trade (e.g. *Melogale orientalis* and *Arctonyx collaris*; Kim 2012, Chen et al. 2015), or exploitation for medicinal and/or witchcraft uses (e.g. *Poecilogale albinucha*, *Mellivora capensis* & *Arctonyx collaris*; De Luca & Mpunga 2013, Duckworth et al. 2016). Some species are afforded legal protection (e.g. *Meles meles* in multiple European countries, *Arctonyx collaris* and *Mellivora capensis* in certain Asian countries; Griffiths & Thomas 1993, Do Linh San et al. 2016, Duckworth et al. 2016), yet illegal persecution remains a threat. Biological resource use also extends to habitat change and forest loss and fragmentation, as resource use has been reported to affect *Meles meles* (Pita et al. 2020) and *Melogale everetti* (Wilting et al. 2016) locally, although this has been comparatively little studied. Habitat change is also considered to be an indirect threat, as it can increase human access into areas that were previously difficult to enter, allowing vehicular removal of wildlife for sale, thus exacerbating the hunting threat, for example, for *Arctonyx collaris* (Duckworth et al. 2016).

Transportation was also frequently reported as a threat for these species, although almost all studies on this threat were focused on *Meles meles* and *Taxidea taxus* (Clarke et al. 1998, Sunga et al. 2017). The intensification and conversion to cultivated land was mostly identified as having a negative impact (e.g. Lara-Romero et al. 2012). However, certain agricultural landscape elements, such as agroforestry systems and hedgerows (Chiatante et al. 2017), could be beneficial sor species such as *Meles meles*.

FUTURE RESEARCH AND CONSERVATION

Once widespread in Europe, *Mustela lutreola* is now classified as Critically Endangered as the species is restricted to a few isolated populations, all facing intense threats. Despite having been extensively studied, the exact reasons for the species' decline remain particularly complex as they combine a number of threats, encompassing invasive species, habitat loss, and pollution (Maran et al. 2016). The case of *Mustela lutreola*, however, remains an exception, as the category of most mustelids in Europe and North America is reported globally as Least Concern by the IUCN. This is partly determined by their large geographical ranges, which often span an entire continent and exceed the threshold for Vulnerable classification, and listing a species as Vulnerable or higher based on range or population size alone without any evidence of decline rarely occurs. Furthermore, in Europe and North America, past declines have often been reversed and recoveries tend to be well understood, if not globally, locally. At a national level, many species have undergone contrasting population trends and are consequently subject to different levels of protection. *Mustela putorius*, for example, was almost driven to extinction through persecution in Britain in the 19th and 20th centuries (Langley & Yalden 1977). A reduction in persecution through the banning of certain trapping methods, legal protection, and reintroductions has resulted in a strong increase in the British population. While thought to have remained fairly constant in continental Europe during the 20th century, recent reports suggest that *Mustela putorius* populations are now declining in most of the continent (Croose et al. 2018). Such national variations within a species' global range can provide insight into identifying primary threats for a species and its ability to recover if threats are addressed. Unfortunately, a paucity of species-specific information inhibits the development and deployment of effective conservation actions for many species, especially in the tropics. The need for action to reverse population declines justifies the necessity to highlight the following key measures, which have proved effective in the recovery of certain species:

- The reduction in persecution, either through legal protection or by the implementation of harvesting regulations, has been crucial in halting the decline and facilitating the recovery of several species. This is particularly true for commercially valued furbearers, notably the *Martes* species (see Guloninae section above) and some Lutrinae species (e.g. *Enhydra lutris*, Doroff et al. 2003).
- Increasing the availability, quality, and connectivity of habitat is likely to have had a role in facilitating the recovery of some species; for example, increases in forestry cover have provided greater habitat availability and connectivity, which may have assisted in the range expansion of *Martes martes* (O'Mahony et al. 2012), and restoring otter habitats has aided re-colonisation by *Lutra lutra* (Schmidt et al. 2012).
- Banning or restricting use of pollutants has been attributed to the recovery of members of the Lutrinae subfamily (e.g. *Lutra lutra*, Ruiz-Olmo et al. 2000).
- Conservation translocations to restore species to parts of their former range have been carried out for Guloninae species (see Guloninae section above), Lutrinae species (e.g. *Lontra canadensis*, Mowry et al. 2015), and Mustelinae species (e.g. *Mustela nigripes* Jachowski & Lockhart 2009), and these generally have high reported success rates when following IUCN guidelines for conservation translocations.
- The restoration and management of prey species has been used as a conservation tool, for example restoring and managing populations of prairie dogs *Cynomys* species as a means of recovering *Mustela nigripes* populations (Truett et al. 2006).
- Controlling the spread of invasive species, which have a deleterious impact on native mustelids, is critical for the long-term viability of these populations. The most urgent example of this is the need to remove and prevent further expansion of invasive populations of *Neovison vison* in areas occupied by *Mustela lutreola* (Maran et al. 2017a). The complete removal of invasive populations of *Neovison vison* is challenging, yet there is a general consensus that *Mustela lutreola* would have gone extinct in further parts of its extant range if intensive control of *Neovison vison* had not been undertaken (Maran et al. 2017b).

The breadth of knowledge about mustelid conservation may help towards the recovery of less-studied declining species by highlighting possible conservation strategies, which could be applied to other species. Such measures, however, are often extremely challenging, and even large amounts of money and decades of conservation effort do not guarantee durable success. Besides, the extent and nature of threats in tropical regions are also likely to differ from those in other parts of the world where conservation measures have proved effective. The combination of unprecedented levels of deforestation with increasing human populations, agricultural intensification, road activity, persecution, water pollution from mining, and other activities may make tropical regions significantly more dangerous for mustelids than other regions. For example, the sustainable reduction in the threat of biological resource use will have to be complex and consider region-specific human socio-cultural needs as different drivers, such as food consumption or cultural beliefs, which motivate the exploitation of small carnivores (Marneweck et al. 2021). This justifies the need to increase the research capacity in these countries and encourage research on targeted species, such as Data Deficient species, accompanied by appropriate advocacy work. As observed in this study, IUCN specialist groups also play a key role in identifying potential threats by facilitating the publishing process for species-specific studies particularly in tropical regions. As suggested by Marneweck et al. (2021), more frequent IUCN Red List assessments are also recommended, as these result in an increase in scientific knowledge, raised awareness, funding and resource allocation, and increased conservation activity (Betts et al. 2020). However, these assessments largely depend on the IUCN receiving sufficient input from experts to perform them.

New threats, for which we do not fully understand the magnitude, are likely to affect mustelids in future. Increased land-use changes have led to more human–wildlife interactions, a prominent source of zoonotic diseases (White & Razgour 2020). As observed during the COVID-19 pandemic, spillover events from humans to wild animals can occur, such as with captive *Neovison vison*, and can further impact wild mustelid populations (Gryseels et al. 2020, Boklund et al. 2021). Climate change is also recognised as a major threat to biodiversity. Evidence on its impact is growing, and effects have already been researched in many taxa (e.g. chiroptera, lepidoptera; Rebelo et al. 2010, Diamond et al. 2011). However, impacts of climate change on mustelids, with the exception of *Gulo gulo*, remain poorly understood.

CONCLUSION

In this review, we documented the conservation category of all mustelid species, and reported the threats that they face according to the IUCN Red List. We found that almost half of mustelids are decreasing, a very high proportion of species that are at risk inhabit the tropics, and biological resource use is the most prominent threat reported. Then, we performed a systematic review to identify reported threats in the scientific literature. The scientific literature was largely biased towards certain species that have undergone major declines in the Northern Hemisphere (e.g. *Lutra lutra*, *Enhydra lutris*), and many seriously threatened species in tropical regions remain poorly studied. The breadth of information available may help us to understand the impact of threats and point towards effective conservation measures for less-studied species. However, increased focus on declining species in the tropics and the impact of new threats, such as emerging diseases and climate change, is also essential to address the decline of mustelid populations.

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We dedicate this paper to the memory of Professor Dame Georgina Mace who died in September 2020 and Professor Richard Shore who died in July 2020. Professor Mace was the driving force behind the IUCN's Red List of Threatened Species that has been the foundation of conservation policy since 1996. Her achievements have had a huge impact on the conservation of species across all major taxonomic groups. Professor Shore was the Science Area Lead for Pollution and Environmental Risk at the Centre for Ecology and Hydrology and President of the Mammal Society in Britain. Professor Shore worked on a multitude of ecotoxicological projects, and his research was pivotal in identifying the risk of rodenticides to *Mustela putorius*.

DATA AVAILABILITY STATEMENT

Data from our study are freely available online at FigShare, https://doi.org/10.6084/m9.figshare.18858344.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s website.

Appendix S1. Results from the two-proportions z-tests for the proportion of threats in the scientific literature and reported by the IUCN.

Appendix S2. Results from the two-proportions z-tests for the proportion of subthreats in the scientific literature.