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A review of depredation modelling across terrestrial and marine realms: State of the art and future directions

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Abstract :

Depredation has become a major concern worldwide as it jeopardises both socio-economic activities and species conservation. While modelling can help to inform the management of these conflicts, effectiveness may be hampered by the complexity of interactions that depredation generates within socio-ecological systems. Based on a systematic literature review, we summarised current practices and identified major gaps and research priorities for depredation modelling. We found that 74% of reviewed studies used statistical models to quantify depredation levels, identify environmental or anthropogenic factors influencing these levels or assess the effectiveness of specific mitigation measures. Only 8% of studies used models incorporating elements related to the three main entities involved in depredation: human activity, depredating species and depredated resource. Such integrated modelling approaches are however crucial to comprehensively assess management trade-offs. Thus, we highlighted future research priorities to comprehensively model depredation and inform the management of human-wildlife conflicts.

Highlights

► We carried out a systematic review to identify relevant approaches to study specific aspects of depredation through modelling. ► We found statistical models to be predominantly used. ► We identified the main factors driving depredation modelling efforts. ► We provided recommendations for effective depredation modelling. ► We highlighted research priorities to comprehensively model depredation.

Keywords : Depredation, modelling, human-wildlife conflict, systematic review, crop damage, attack on livestock, fisheries and aquaculture

1. Introduction

The acceleration of human population growth in the second half of the 20th century has led to an intensification of conflicts between people and wildlife, commonly called human-wildlife conflicts (Nyhus, 2016; Woodroffe et al., 2005). Human-wildlife conflicts include threats posed by wildlife to human life, economic security, or recreation as well as negative human perceptions or actions against wild populations considered as a threat for human safety, health, food, and infrastructure (e.g. culling of top predators such as wolves; see overview in Nyhus, 2016). Depredation, a behaviour developed by wild animals when feeding on resources raised or exploited by humans, is at the root of many of these conflicts (Sillero and Laurenson, 2001). Depredation has been reported worldwide from both terrestrial and marine ecosystems, and includes crop raiding by terrestrial herbivores (Barnes and Douglas-Hamilton, 1982), attacks on livestock by terrestrial predators (Dickman and Hazzah, 2016), and marine predators (mainly sharks and marine mammals) removing fish from fishing gear or aquaculture farms (Mitchell et al., 2018; Read, 2008; Tixier et al., 2021).

Depredation can induce complex changes in socio-ecosystems by affecting both the depredating species and the resources raised or exploited by humans (i.e. crop, livestock, farmed fish, wild fish). The main effects of depredation are threefold. First, it can lead to direct interactions between the depredating species and humans or equipment, exposing depredating individuals to risks of death or injuries through lethal retaliation/control or incidental capture (Azevedo et al., 2017; Dans et al., 2003). Second, as depredation facilitates access to food, it can change the ecological role of the depredating species and alter natural ecosystem interactions (Clavareau et al., 2020). Third, depredation can compromise the profitability of human activities by decreasing yield or damaging equipment (Dickman and Hazzah, 2016; Wickens et al., 1992). For instance, killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) were found to remove an estimated 15 M US$ worth of fish from fishing lines every year in subantarctic fisheries (Tixier et al., 2020). In the United States, the estimated cost of the white-tailed deer (*Odocoileus virginianus*) raiding on crops was 619 M US$ in 2001 (NASS, 2002).

While ecological modelling (e.g. Lotka-Volterra prey-predator dynamic modelling) historically targeted theoretical questions rather than practical applications for natural resource management, enhanced computing facilities have facilitated the emergence of a diversity of modelling approaches that now routinely support decision-making for environmental and fisheries management (Badham et al., 2019; Colléter et al., 2015; Fulton et al., 2011; Geary et al., 2020). Similarly, a range of socio-ecological modelling approaches have emerged to characterise the complex and multi-faceted aspects of depredation. These approaches are diverse, and include studies using, for instance, statistical approaches such as generalized-linear-mixed models (Kiffner et al., 2021), Bayesian isotope mixing models (Reitsema et al., 2020) or hidden Markov models (Mul et al., 2020). Mechanistic approaches have also been developed such as economic models (Loch-Temzelides et al., 2020) or mass-balance food web models (Clavareau et al., 2020). Conceptual models have also been used (Beck et al., 2019). Certain approaches can integrate heterogeneous data sources to capture processes and interactions between major environmental, biological, and socio-anthropogenic components of socio-ecosystems. In particular the data may concern the three main components of depredation: human activity, depredating and depredated species, but also information regarding the ecosystem that hosts these three conflict actors or the mitigation methods in place. In a depredation context, modelling can thus provide valuable means to test hypotheses and identify influential drivers of complex dynamics, to assess the consequences of alternative management scenarios and to guide interventions to enhance socio-ecosystem resilience and sustainability (Dambacher et al., 2015; Gourguet et al., 2021; Marzloff et al., 2016). However, given the complexity and diversity of impacts associated with depredation, it can be difficult to choose the appropriate modelling approach, which not only depends on the depredation context but also on data availability (Tixier et al., 2021).

In this study, based on a systematic literature review across terrestrial and marine cases of depredation, we summarise the current use of modelling approaches and identify approaches that are suitable to study specific aspects of depredation. To this end, we refined a systematic classification of all relevant papers according to (1) modelling approaches, (2) study purposes, as well as (3) types of socio-ecological components explicitly considered. Identified knowledge gaps lead us to the proposal of future depredation research and modelling directions, including the integration of all available knowledge into interdisciplinary models that comprehensively capture the key aspects of socio-ecological systems affected by depredation. Such integrated models are critical to inform effective socio-ecosystem management when facing human-wildlife conflicts.

2. Methods

2.1. Systematic review process

We conducted a systematic review of the scientific literature covering studies that used modelling to study depredation. Based on a number of initial trials to test for the sensitivity of the literature search according to specific terms, we finalised a combination of search terms as follows. We used (*a*) "depredation" as the primary search term and combined it with specific terms for depredation on four resource types. For depredation on crops, we added (*b*) 'crop raiding' OR 'crop damage', for depredation on livestock (c) 'livestock attack' OR 'livestock damage', for depredation on farmed fish (d) 'stock attack' OR ('aquaculture' AND 'interaction'), and for depredation on fishery catches (e) 'catch remov*' OR 'catch damage'. These specific terms were combined with (f) 'wildlife' OR 'predat* to focus on damage caused by wild species, as well as (g) 'mammal*' OR 'shark*' commonly observed depredating in the marine realm. Terms such as (h) 'law', 'chemi*', 'nest*' or 'bacteri*' were excluded to restrict the search to publications addressing depredation in a human-wildlife conflict context. To focus the search on studies that used a modelling approach, we added (i) 'model*' to the set of search terms. This resulted in the following final search equation:

$$\left((a\ OR\ b\ OR\ c\ OR\ d\ OR\ e\ )\ AND\ (f\ OR\ g)\right)\ NOT\ h\ AND\ i$$

which was used to search in abstracts, keywords and titles of studies published between 1995 and 2021 (April 20) and referenced by the Web of Science (WoS) in all fields.

2.2. Preliminary paper screening, data coding and extraction

The search equation yielded a total of 774 publications (cf. fill list provided in **Table B1**), among which 312 (40%) were considered relevant for this review based on initial screening of titles and abstracts, as they were indeed relying on modelling approaches to study depredation. The remaining publications were discarded either because modelling was only mentioned or discussed (rather than effectively used as a methodology), or because they were found to focus on natural predation rather than depredation.

For each of the retained 312 publications, we collected the following information: type of human activity and nature of the exploited or produced resource subject to depredation; realm (terrestrial or marine); depredating species taxa; geographic location of the case study (countries for terrestrial and FAO major fishing areas for marine cases); primary purpose of the study; and, type of modelling approach(es) and type of model(s) used as well as the variables captured in the model(s).

To categorise identified publications according to their dominant modelling purpose, we used the major socio-ecological aspects of depredation identified in Tixier et al. (2021) to define six categories: (1) the "*perception*" category for studies investigating human perception of depredation or depredating species; (2) the "*depredating species ecology*" category for publications assessing either the distribution, diet and population size or dynamics of depredating species; (3) the "*factors influencing depredation*" category for studies that mainly focused on the environmental or anthropogenic factors influencing depredation or the number of depredating individuals; (4) the "*quantification of depredation*" category for publications that either assessed the risk (probability), rate or frequency of depredation events, or the change in yield caused by depredation (without quantifying socio-economic consequences); (5) the "*socio-economic consequences*" category for publications focusing on the financial or employment consequences of depredation (i.e. profitability or sustainability of food production or exploitation activities); (6) the "*mitigation*" category for publications investigating ways to mitigate depredation or to assess the effectiveness of mitigation management measures.

Modelling approaches were first grouped into three broad categories, namely: statistical, mechanistic or conceptual; and then further assigned to subcategories as follows. Statistical models were further categorised as simple (e.g. regression) or advanced statistical models (e.g. hidden Markov models, machine learning). Mechanistic models were categorised into population dynamics models, individual-based models, trophic models, qualitative models and economic models. No subcategories were defined for conceptual models.

We assessed the degree of integration of the three components involved in depredation (human activity, depredating species and depredated resource) into the models used in the reviewed publications. For this, the variables used to capture aspects of each of these three main components were identified and schematically represented (**Figure 1**). Variables considered relating to humans and their activities included individual perception of the conflict (i.e. of depredation risk, or of depredating species), economic aspects (costs, profits), personal information (age, gender, ethnicity), social data (wealth, education, religion, occupation) and activity details (gear or agriculture technique, operation characteristics, number of farms or boats owned, yield and effort) (**Figure 1**). Integration of the depredating species and/or the depredated resources occurred via variables related to the natural diet of the depredating species, spatial distribution, presence-absence of the species, population size (abundance or density), parameters of population dynamics (mortality, breeding and growth rate) or population structure (i.e. life stage or age, body mass and sex) (**Figure 1**). Depredation is commonly expressed as loss rate, frequency of events, or probability of occurrence. Concerning management, mitigation is characterized by the use of physical devices or strategic methods. (**Figure 1**). The list of possible environmental variables included temperature, moon phase, water chemistry, study area protection status, bottom topography (slope, depth, altitude), habitat characteristics (vegetation type, vegetation coverage, water surface and distance to coast in marine realm), and climatic conditions (average rainfall, season, weather, cloud cover) (**Figure 1**). Lastly, variables considered relating to anthropogenic stressors were human population size, activity category (recreational or professional), and land use characteristics (agriculture coverage, road and settlement density) (**Figure 1**). Category details for all analysed papers are available in Supplementary Material **Table B1**, so we do not comprehensively cite relevant papers in the following sections.

3. Results

3.1. Global scope of depredation modelling

The number of publications using modelling to study depredation has dramatically increased since 1996, with 85% of the 312 reviewed publications published after 2010 (**Figure A1**). Terrestrial depredation was studied in 263 publications (84%), among which 53% focused on livestock depredation, 42% on crop depredation, and 5% on both (**Figure 2**). Only 49 publications (16%) studied marine depredation, 76% of which focused on depredation on fishery catches, 22% on depredation on farmed fish, and 2% on both (**Figure 2**). Overall, 96 species were identified as depredating. These species belonged to 12 orders, including 14 bird species (Anseriformes, Gruiformes, Passeriformes, Pelecaniformes, Suliformes), 74 terrestrial mammals (Artiodactyla, Carnivora, Primates, Proboscidea, Rodentia), 7 marine mammals (Cetacea, Carnivora) and one cephalopod (Octopoda).

The reviewed studies used a modelling approach to address depredation cases distributed across 61 countries around the world (**Figure 3**). In the terrestrial environment, 55 publications (22%) studied cases within the United States, covering 27 federal states, of which nearly half (19) studied grey wolf (*Canis lupus*) depredation on livestock. Other countries that concentrated high research effort using modelling included India and Nepal (34 publications). The majority (25, 74%) of these 34 publications investigated depredation on livestock by big cats, including tigers (*Panthera tigris*), leopards (*Panthera pardus*), snow leopards (*Panthera uncia*) or Indian lions (*Panthera leo persica*). Big cat depredation has also been studied in Tanzania (4), where it involved African lions (*Panthera leo*), and Brazil (7), where it involved jaguars (*Panthera onca*) and pumas (*Puma concolor*). In Italy, six studies focused on grey wolf depredation on livestock and six on wild boar (*Sus scrofa*) depredation on crops. In Tanzania, the case of elephants (*Loxodonta africana*) depredation on crops was investigated in 3 publications.

In the marine environment, the reviewed studies were distributed across 12 FAO major fishing areas (**Figure 4**). Most studies using models (9 publications, 19% of publications on marine depredation) focused on depredation in the Northeast Atlantic (FAO area 27), mainly depredation by harbour seal (*Phoca vitulina*) on salmon fisheries. In seven publications (15%), models were used to study depredation by killer whales and sperm whales on toothfish fisheries in the Southern Indian Ocean (FAO area 58). Another six publications (13 %) used models to study depredation by bottlenose dolphins (*Tursiops truncatus*) on farmed fish and fishery catches in the Mediterranean and Black seas (FAO area 37). There were five publications from the Northeast Pacific and Western Central Atlantic (FAO area 67 and 31 respectively). Killer whale and sperm whale depredation on sablefish (*Anaploma fimbria*) was investigated in the Gulf of Alaska and that of double-crested cormorant (*Phalacrocorax auritus*) on farmed catfish (*Ictalurus spp.*) in the Mississippi**.**

3.2. Modelling approach and study purpose

Most reviewed studies used statistical models for both terrestrial and marine cases of depredation (263 publications, 84%), followed by mechanistic models (39, 13%) and conceptual models (6, 1%) (**Figure 5**). The majority of statistical modelling studies (239 publications, 89%) used simple regression models (e.g. Kiffner et al., 2021), followed by more complex models such as machine learning (21, 8%, e.g. Reitsema et al., 2020) and hidden Markov models (3, 1%, e.g. Mul et al., 2020). Mechanistic models were mainly economic models (16, 41%; e.g. Clark et al., 2020b), population dynamics models (6, 15%; e.g. Brewster et al., 2019) and individual based models (11, 28%; e.g. Simon and Fortin, 2020) (). Trophic (5, 12%; e.g. Clavareau et al., 2020) and qualitative models (1, 3%; Szymkowiak and Rhodes-Reese, 2020) were employed to a much lesser extent. Conceptual models have only been used to study terrestrial depredation (6, e.g. Beck et al., 2019.

The main purpose of the reviewed publications was to determine the factors influencing the magnitude and extent of depredation (127 publications, 41%; **Figure 5**). A number of models, such as regression models, were used to quantify how the occurrence and severity of depredation varied spatially and seasonally. For instance, African lion depredation on livestock in Tanzania was found to be explained by vegetation productivity and proximity to surface water (Beattie et al., 2020), while killer whale depredation on fishery catches in Uruguay varied with distance to the coast (Passadore et al., 2015). The second most common study purpose was the quantification of losses due to depredation (28%). Application of generalized additive models (GAM) revealed that whale depredation removed 30% of total catches from the fishery around Crozet islands (southern Indian Ocean) (Tixier et al., 2020). Generalized Linear Models (GLM) showed deer and elk depredation affected 7% of safflower plants in Utah (Haney and Conover, 2013). Testing the effectiveness of mitigation measures was the third most common study purpose (18%). For this, models were mainly used to compare the frequency or intensity of depredation events with and without mitigation measures or among different mitigation measures. For example, GLMs were used to test the effectiveness of fences or protective enclosures in reducing crop depredation by elephants in Tanzania (Scheijen et al., 2019), and GAMs to test the effectiveness of deterrent devices in reducing bottlenose dolphin depredation on coastal gillnet catches (Waples et al., 2013). To a lesser extent (8% of the reviewed publications), models were used to investigate the ecology of the depredating species, in particular their spatial distribution (Burr et al., 2020; Giefer and An, 2020). Models were also used to assess the socio-economic consequences (4%) and the human perception (4%) of depredation. Human perception of depredation or depredating species was mostly studied in the context of implementing new mitigation measures, re-introducing emblematic species or translocation. For example, a linear model was used to explore attitudes towards the proposed translocation of blue sheep into Sagarmatha National Park to reduce depredation of livestock by snow leopards (Hanson et al., 2020).

Certain objectives were addressed with specific modelling approaches. Depredation was mainly quantified out using statistical models, specifically regression models (86%) and machine learning (14%; **Figure 5**). In contrast, socio-economic consequences were primarily studied with mechanistic models (77%), which comprised economic models (60%), individual-based models (20%), population dynamics models (10%) and trophic models (10%).

3.3.System components and variables

Among the three main components involved in all depredation conflicts, the depredating species were reported in most reviewed publications (268 publications; 86%), followed by the depredated resource (159; 51%) and humans (87; 28%). Among variables incorporated in models, variables related to environmental conditions were considered in most reviewed publications (176; 56%), followed by management (67; 21%), anthropogenic pressures (61; 19%), and interacting species (preys or predators of the depredated resources or the depredating species) (32; 11%). The most commonly studied variables for each of the three components were consistent across the terrestrial and marine realms (**Figure 6**). For depredating species, depredation behaviour was most commonly modelled (39%), either in the form of a depredation rate, occurrence or frequency of events. For depredated and interacting species, population size expressed as abundance or density was most commonly considered, respectively in 65 (20%) and 26 publications (8%). For depredating species, population size was also frequently accounted for (56, 18%). For instance, prey abundance or shortage of wild food sources explained common dolphin depredation in the Azores (Cruz et al., 2016) and wolf depredation on livestock in Portugal (Pimenta et al., 2018). As for environmental conditions, habitat was the most commonly studied explanatory variable (45%), followed by topography (13%) (**Figure 7**). Like population size, habitat and topography were primarily used to explain occurrence and intensity of depredation, e.g. forest coverage and slope in the case of elephant depredation on crops (Ngama et al., 2019). The occurrence (30%) and population dynamics parameters (10%) of the depredating species were the variables most commonly modelled in the marine realm (49 publications), and about half as often in terrestrial studies (14% and 5% of 263 publications, respectively) (**Figure 6**). For instance, when studying the causes of seal depredation, their bycatch mortality was also considered (Cosgrove et al., 2015). Conversely, in the terrestrial realm, population structure of the depredating species (6%) and human related variables such as social (6%) and personal information (6%), and perception (3%) were more frequently considered than in the marine realm (2%, 2%, 0% and 0%) (**Figure 6**). This was for example the case in a study addressing the translocation of blue sheep (*Pseudois nayaur*) to reduce livestock depredation by snow leopards (Hanson et al., 2020). The effect of the protection status of the study area was frequently investigated in terrestrial modelling studies (22 publications), while none of the marine studies did so. Anthropogenic pressure information was most commonly modelled via human population size or converted land (33 publications) (**Figure 7**). Both variables were mainly used to identify factors influencing depredation or for creating depredation risk maps.

In the marine realm, depredating species and depredated resources were generally characterised by different variables. Presence-absence, population size and population dynamics parameters were more frequently used for the depredating species (30%, 20% and 10% of the 49 marine studies, respectively for each type of variable) than for the depredated resource (respectively 8%, 8% and 4%) (**Figure 6**). Presence-absence of the depredating species was mainly used to identify factors influencing its spatial distribution (e.g., Bonizzoni et al., 2021; Mul et al., 2020). Using a generalized additive model, Bonizzoni et al., 2021) found that trawling influenced the dolphin distribution in the Adriatic Sea and increased the chances of encountering them 4.5-fold. Conversely, population structure (10%) and taxonomic affiliation (10%) of the depredated species were more commonly taken into account than for the depredating species (each 2%). Briceño et al. (2015) found that in a South Australian fishery the risk of pot predation by the Maori octopus (*Pinnoctopus cordiformis*) increased with rock lobster (*Jasus edwardsii*) body size and was higher for males.

3.4. Integration of system components into models

Among the 312 reviewed publications, 33% used models that incorporated variables describing both the depredating species and the depredated resource, while 32% considered variables for the depredating species only (**Figure 8**). Models considering variables for both the human activity and the depredating species were found in 13% of publications, consisting of 20 terrestrial and 21 marine studies.

In only 8% of the reviewed publications, models incorporated variables from all three major components of depredation systems, including 18 terrestrial and 6 marine studies (**Figure 8**). In the terrestrial depredation studies, statistical models were primarily used to map the depredation risk for human activities, or guide conservation actions for the depredating species. Three of these studies estimated the probability of depredation or identified factors influencing depredation levels or the socio-economic consequences of depredation to inform on possible mitigation measures for depredation on livestock by snow leopards following the re-introduction of this species classified as “vulnerable” on the IUCN Red List (Chetri et al., 2019; Din et al., 2019; Loch-Temzelides, 2021). For instance, Chetri et al. (2019), using GLMMs, found that the probability of livestock loss to snow leopards increased with herd size, thus affecting owners of large herds more frequently. Three other publications used conceptual and regression models to identify factors influencing the levels of lion depredation on livestock and to assess ways to attenuate the conflict through changes in human perception towards the depredating species (Beck et al., 2019; Dunnink et al., 2020; Hazzah et al., 2013). For example, (Hazzah et al., 2013) demonstrated that higher education was associated with more positive perceptions towards depredating lions and lower propensity of people to kill them as an act of retaliation to depredation. Three publications used regression models to identify areas with high risk of depredation to inform on the implementation of mitigation based on spatial adjustments of the human activity involved. These models combined variables describing characteristics of the human activity with information on the spatial occurrence of depredation, the depredating species and the spatial density of the depredated resource (Karanth et al., 2012; Pimenta et al., 2018; Treves et al., 2004). For instance, in Wisconsin, wolf depredation on livestock was explained by farm size and road density (Treves et al., 2004). In the marine environment, only two publications investigated the influence of environmental factors, species composition of the fishing catches, fishing yield and fishing gear type on the levels of marine mammal depredation using regression models (Cruz et al., 2016; Pardalou and Tsikliras, 2020).

4. Discussion

Human-wildlife conflicts caused by depredation represent a worldwide issue both in the terrestrial and marine environments and are likely to intensify in the coming decades. Based on our systematic literature review, we identified the main factors driving modelling efforts, considered the relevance of existing approaches according to case study specifics and data availability, and highlighted future research priorities to more comprehensively study depredation and inform management.

4.1. Depredation modelling studies are over-represented for emblematic and traditional case studies and simplistic for the depredating species

Various models have been applied to numerous cases of terrestrial and marine depredation worldwide. However, scientific efforts tended to concentrate on certain regions or taxa. In addition to the severity of depredation, factors such as the human activity subject to depredation becoming unviable, as well as the conservation status of the depredating species and the state of the exploited resource, may have contributed to an enhanced focus on certain cases.

While estimating economic losses or assessing the viability of human activities impacted by depredation represent central modelling objectives, a large research effort has focused on a restricted set of case studies associated with depredated resources of high socio-economic importance. In the marine realm, much modelling effort has been directed towards estimating the losses caused by depredation on fishery catches for high value species such as salmon (*Salmo salar*) in the Baltic Sea and Patagonian toothfish (*Dissostichus eleginoides*) in subantarctic waters (Fjälling, 2005; Grilly et al., 2015; Oglend, 2013; Tixier et al., 2020, 2019, 2016). Beyond high-value species, well-represented case studies related to food industry sectors of importance in the global or regional economy. For instance, large modelling efforts have been dedicated to study depredation on livestock in the United States and in Brazil, which are two of the world’s largest meat producers, (Ritchie et al., 2017). The large number of these well-documented case studies might reflect the ability of major food industries to invest in research and consolidate relevant datasets to model the major factors, such as losses to depredation, that drive their productivity and profitability. In these well-studied cases, modelling results overall suggest that depredation and its subsequent economic losses can jeopardise the profitability and long-term resilience of individual businesses (i.e. a fishing vessel, or a farm) without necessarily compromising the viability of a whole food production sector (i.e. a fishery, or regional farming production). Thus, modelling outputs mostly support decision-making at the individual or business scale than at the broader industry level. For instance, several studies have quantified how depredation differentially impacts individuals depending on their practises, techniques, perception of the conflict, adaptation strategies, or on their geographical location (Tixier et al., 2020).

Much modelling effort has also been invested to study depredation by depredating species of high conservation interest. Indeed, a large proportion of the reviewed publications focused on vulnerable species such as grey wolf (least concern), snow leopard (vulnerable), lion (vulnerable), harbour seal (least concern), killer whale (data deficient) and sperm whale (vulnerable; https://www.iucnredlist.org). Several studies have modelled how responses or measures to minimise depredation by these species may jeopardise ongoing conservation initiatives to restore populations of these predators. Because depredation conflicts can lead to negative attitudes of people and retaliation towards these taxa (Salerno et al., 2020), a number of modelling studies aimed at understanding factors that affect human perception of depredating species. With the aim of respecting ongoing conservation efforts targeted at emblematic depredating species, many of the reviewed studies characterised the effectiveness of non-lethal measures to attenuate the levels of depredation, e.g. using fences (Kiffner et al., 2021), acoustic (Waples et al., 2013) or spatial activity adjustments (Chetri et al., 2019; Din et al., 2019; Loch-Temzelides, 2021).

Despite a growing number of publications, the study of marine depredation remains rare compared to terrestrial cases. This is somewhat surprising given that depredation affects coastal and offshore fisheries using a broad range of fishing techniques worldwide (Gilman et al., 2007; Mitchell et al., 2018). Terrestrial depredation has been known since the beginning of agriculture several millennia ago, with for instance, the case of elephant depredation in Africa (Barnes and Douglas-Hamilton, 1982). This early knowledge may explain the greater number of publications applying modelling to terrestrial depredation. Marine depredation has only emerged as a problematic around the 1970s, concomitantly with the global expansion of fisheries and the increasing application of non-lethal mitigation measures in a conservation context (Hamer et al., 2012; Mitchell et al., 2018; Read, 2008; Tixier et al., 2021). The study of depredation in the marine environment is therefore relatively recent and this might imply limited availability of suitable data. Moreover, data acquisition is generally more difficult in the marine environment. Typically, depredation on fishery catches is not systematically detected as predators may remove fish from the fishing gear without leaving any visible evidence for fishers to know that it happened (Richard et al., 2020; Tixier et al., 2020). As a consequence, data on marine depredation are mainly qualitative (Peterson and Hanselman, 2017; Werner et al., 2015). Thus, consolidating data collection on marine depredation will be pivotal to future modelling efforts.

In most modelling studies, the depredating species was only implicitly captured as a rate or a probability of depredation. Further, depredating species were predominantly represented as a source of negative impacts on humans, including loss of income, destruction of buildings, physical injury or human mortality (Locke, 2013; Shoreman-Ouimet and Kopnina, 2015). This might arise because human-wildlife conflicts were most commonly modelled from an anthropocentric viewpoint, but also due to knowledge and data gaps about the ecology of the depredating species. As a consequence, only a handful of studies (e.g. Burr et al., 2020; Giefer and An, 2020) accounted for spatio-temporal variability in the occurrence or population size of the depredating species to explain the severity of the conflict or to quantify losses. The number of depredating individuals within populations may increase as a result of an increase of population size thanks to ongoing conservation initiatives and/or more and more individuals developing depredation as a new behaviour, for instance through social learning (e.g. Schakner et al., 2014). This highlights the importance of improving the knowledge on the ecology of depredating species as a key information needed to dynamically project population changes and wider long-term consequences of depredation. Such projections of long-term dynamics will have to account for both the negative and positive effects that depredation may have on life history traits of individuals, with on one hand, risks associated with humans or human equipment- and on the other hand, benefits from food intake at low foraging effort. For instance, studies using long-term data have shown that depredation could negatively impact the survival rate of killer whales by exposing individuals to lethal practices (shooting with firearms) used by illegal fishers but also positively influenced the calving rate of females by providing a facilitated access to fish prey (Tixier et al., 2017, 2015).

It should be noted that our review has certain limitations, and although we have tried to include as many papers as possible with a varied corpus of search words to define depredation, some may have been missed. Furthermore, the results of this study are limited to papers referenced in the Web of Science between 1996 and April 2021. However, we expect that the overall conclusions drawn from this study, which includes over 300 papers, will not be greatly affected.

4.2. Recommendations for depredation modelling

A diversity of modelling approaches has been applied to understand or predict processes or dynamics related to depredation (**Table 1)**.

Depredation involves at least three components: human activities, depredated and depredating species. The processes involved and hence potentially modelled, are therefore numerous and diverse. The main effects of depredation are also threefold: direct negative impacts of depredation on humans or equipment, alteration of natural ecosystem interactions and reduction of the profitability of human activities. In a given depredation situation, it is therefore essential to first identify the major processes and effects at play. This first step can be carried out using conceptual models, which have proven valuable to summarise relevant case-specific processes (Nieva and Wegmann, 2002) . Creation of a conceptual model can provide a structured way to evaluate the availability of relevant data, identifying key knowledge gaps and prioritising field observations and sampling efforts. Indeed, quantification of key aspects of depredation conflicts is generally limited by lack of data and sparsity of observations rather than by methodological challenges.

In a data-poor context, which represent a large proportion of marine depredation cases as well as numerous understudied or emerging terrestrial cases, qualitative modelling (methods derived from Puccia and Levins' "loops analysis"; Dambacher et al., 2003; Puccia and Levins, 1985) seems an appropriate second step for analysing conceptual models for which the signs of the relationships between system components have been specified, though not their strengths. Specifically, qualitative modelling offers a way for assessing the direction (positive, negative, null) of the effects of alternative adaptation strategies on human economic benefits and wellbeing. The approach has been used to help assess the potential effectiveness of adaptation strategies in responses to scenarios of increasing depredation (Szymkowiak and Rhodes-Reese, 2020). Further, a qualitative modelling study of marine depredation revealed in which ways the expected effects of depredation depended on the relative importance of different interacting ecological processes (Clavareau et al., 2023).

In a data-rich context, which generally corresponds to emblematic or traditional case studies with much long-term research and data collection efforts, as a second step, both statistical and process-based models can provide useful complementary insights into key elements of the depredation conflict. Statistical methods can help to fill basic knowledge gaps related to depredation, such as assessing the consequences of depredation on the production of natural resources and on human activities (Haney and Conover, 2013; Tixier et al., 2020), characterising the environmental or anthropogenic drivers that enhance depredation (Beattie et al., 2020; Briceño et al., 2015; Passadore et al., 2015), assessing effectiveness of mitigation measures (Dunnink et al., 2020), or mapping depredation risk (Denninger Snyder et al., 2021; Treves et al., 2011). If the objective is to estimate depredation rates or consequences on impacted industries, statistical approaches appear appropriate, e.g. GLMMs allowing random effects to be accounted and GAMs for non-linear relationships (Haney and Conover, 2013; Tixier et al., 2020). However, they are less suitable to jointly quantify multiple interacting aspects of the depredation conflict. Simple statistical models are therefore not recommended for holistic studies for which mechanistic models seem more appropriate.

Indeed, mechanistic models can explicitly capture how interactions between relevant processes and variables can drive responses and dynamics across various scales and components in depredation conflicts. For instance, agent-based models can mechanistically capture interactions between multiple socio-ecological components and account for differences between individual or groups of individuals. They have for example helped to assess the potential role of education in reducing depredation conflicts with bears (Marley et al., 2017). Depredation also impacts human activities socio-economically. On one hand, induced costs can be direct, caused by the loss of produced or exploited resources. On the other hand, they can be indirect when they are (i) related to additional effort required to prevent depredation or protect the resource, (ii) to additional production or exploitation efforts to compensate for losses and maintain activity yield, or (iii) to damages caused to equipment. It is therefore essential to quantify direct and indirect costs, notably to assess the sustainability of the activities concerned. For this specific purpose bio-economic models are the most appropriate. Bio-economic modelling has been used for instance to explore the impact of alternative fishing strategies and levels of depredation on the revenues of fisheries (Trijoulet et al., 2018).

A range of modelling approaches can be applied to capture broader consequences of depredation on socio-ecosystems, most likely as a third step once specific aspects have been studied using more focused statistical or mechanistic models. Wider trophic consequences can be studied using available software platforms such as Ecopath with Ecosim (EwE, Christensen and Walters, 2004). For instance, a recent marine application of EwE quantified the additional mortality caused by depredation by marine mammals on other ecological groups (Clavareau et al., 2020). In contrast, there is a lack of readily available modelling platforms for capturing the multiple feedbacks between humans, depredating species and resources. For this, extensions of the existing bio-economic modelling platforms reviewed by Nielsen et al. (2018) in the context of fisheries and marine socio-ecosystems modelling might be worth developing.

4.3. Modelling feedbacks in depredation systems to support decision making

While statistical and mathematical modelling can effectively guide natural resource management, practical contributions of most depredation modelling studies to tactical or strategic management of depredation conflicts remain limited. Because depredation modelling studies still mostly attempt to fill basic knowledge gaps, only few publications considered interactions between human activities subject to depredation, depredated resources and depredating species, i.e. the three main components. Future development of depredation models ought to capture the essence of this multi-species conflict involving depredating species and natural resources exploited by humans. Specifically, accounting for multiple feedbacks acting over a range of spatial and temporal scales will be crucial to better understand and predict the dynamics of depredation-impacted socio-ecosystems: (1) direct depletion of resources by depredation not only induces losses but can also trigger compensatory processes or reactions by humans; (2) both facilitated access to food and mitigations measures can modify life history parameters of depredating populations (e.g. mortality, growth rate, fecundity); (3) the diet of depredating species may be considerably altered, especially when the depredated resource is not part of their natural diet, resulting in a release of pressure on their wild prey; and so on. More broadly, the modification of life history parameters and pressures related to exploitation or predation themselves generate cascading effects that can modify ecosystem functioning. Moreover, most depredating species are higher trophic level species such as big cats, large sharks and marine mammals, and change in predation pressures from these top-predators are likely to generate greater top-down cascading ecosystem effects than changes from meso-predators (Newsome et al., 2015; Oro et al., 2013). Cascading effects, the reduction of yield, the damage to equipment and the well-being of humans can in turn impact the viability of human activities (Dickman and Hazzah, 2016; Wickens et al., 1992). Within human societies, complex feedback can also contribute to long-term dynamics as for instance depredation-impacted primary industries may defend and promote their interests against the tourism industry or conservation-minded associations, who likely value the restoration of wild predatory populations.

Even when accounting for different dimensions of depredation as explanatory factors (i.e. humans, depredating species or depredated resource), so far modelling studies tended to only estimate outcomes related to one single aspect of the issue, such as conservation status and human perception of the depredating species (Beck et al., 2019), assessment of socio-economic consequences of depredation for primary industries (Brewster et al., 2019; Clark et al., 2020a), effectiveness of mitigation measures (Dunnink et al., 2020), or human adaptation when exposed to depredation (Szymkowiak and Rhodes-Reese, 2020). Thus, while a small subset of models accounts for diverse aspects of depredation, most reviewed studies had a single aim and did not assess trade-offs between conservation status of the depredating species and socio-economic viability of human activities that rely on the depredated resource. Thus, future development for depredation modelling should aim to comprehensively assess the consequences of management interventions or future scenarios for the exploited resources, the depredating species and the human activities that directly or indirectly interact with them. Participatory modelling approaches (e.g. Comod, or participatory modelling.org; Hedelin et al., 2021; Voinov et al., 2018, 2016; Voinov and Bousquet, 2010) will for instance be valuable to engage different stakeholder groups (conservationists, food industry and managers) in refining the scope of future model development, and to more broadly identify the multi-facetted variables and values at stake when modelling depredation conflicts. Beyond improving the relevance of the modelling for decision-making, engaging stakeholders along the different iterative steps of model development can yield additional benefits by promoting knowledge transfer within and between groups (Le Page et al., 2014). For instance, farmers or fishers might directly learn from successful peers about how to accept or best adapt to depredation or, confronting conflicting interests (such as conservation of depredating species *versus* maintaining productivity of the primary industries) can contribute to easing conflicts between different stakeholder groups.

5. Conclusion

In conclusion, although depredation modelling has increased over the last decade, it often focused on emblematic or traditional cases, particularly those of high socio-economic or conservation significance. Noticeably, disparities between terrestrial and marine depredation modelling reflect differences in data availability and historical knowledge.

A number of recommendations for effective depredation modelling emerged from this analysis. Conceptual models can summarise fundamental understanding, which combined with qualitative modelling will provide insights on the impacts of changes, in the ecosystem or management, when data are scarce. Data-rich contexts can serve as pilot cases to develop detailed statistical or mechanistic models, which capture the complexity and interactions between the three main entities involved in depredation. The integration of broader feedback loops, encompassing the complex links between human activities, depredating and depredated species, will be essential for holistic modelling.

Engaging stakeholders through participatory modelling can refine the scope of modelling, improve the relevance of decision-making, and encourage knowledge exchange. Finally, the development of integrated models will make it possible to study human-nature conflicts in their entirety and will help inform management of the ecosystems concerned to reduce human-wildlife conflicts.

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Table 1. Summary of modelling approaches for studying depredation with examples from the literature review. System components correspond to D depredating species, R depredated species, H humans.

Modelling objectives	**System components captured**	**Category**	**Model type**	**Examples**
Structured synthesis of drivers of human-wildlife conflicts	DRH	Conceptual	-	Beck et al., 2019; Shaffer et al., 2019
Qualitative analysis of factors driving human perception and adaptation strategies to depredation	RH	Conceptual	-	Amit and Jacobson, 2017
Assessing the consequences of depredation on production of natural resources and human activities	R or DH	Statistical	Multivariate model, e.g. GLM, GAM	Haney and Conover, 2013; Tixier et al., 2020
Characterising the environmental or anthropogenic drivers that enhance depredation	D or R or DH	Statistical	Univariate model, e.g. linear regression, regression trees or Multivariate model, e.g. GLM	Beattie et al., 2020; Briceño et al., 2015; Passadore et al., 2015
Mapping of depredation risk	DR or D	Statistical	Spatial statistical model, e.g. GAM, geostatistics	Denninger Snyder et al., 2021; Treves et al., 2011
Assessment of mitigation measures effectiveness	DRH	Statistical	Multivariate model, e.g. GLM, GLMM	Dunnink et al., 2020
Determining abundance and natural distribution of depredating species	DR or D	Statistical	Univariate model, e.g. linear regression or Multivariate model, e.g. GLM; GAM	Burr et al., 2020; Giefer and An, 2020
Quantifying economic impact	DH or DRH	Mechanistic	Bio-economic	Holma et al., 2014; Skonhoft, 2017
Assessment of direct and indirect effects of depredation on ecosystem components and human activities	DRH	Mechanistic	Ecosystem model Ecopath	Clavareau et al., 2020
Assessment of effect of alternative adaptation strategies on human economic benefits and wellbeing	DRH	Mechanistic	Qualitative model	Szymkowiak and Rhodes-Reese, 2020

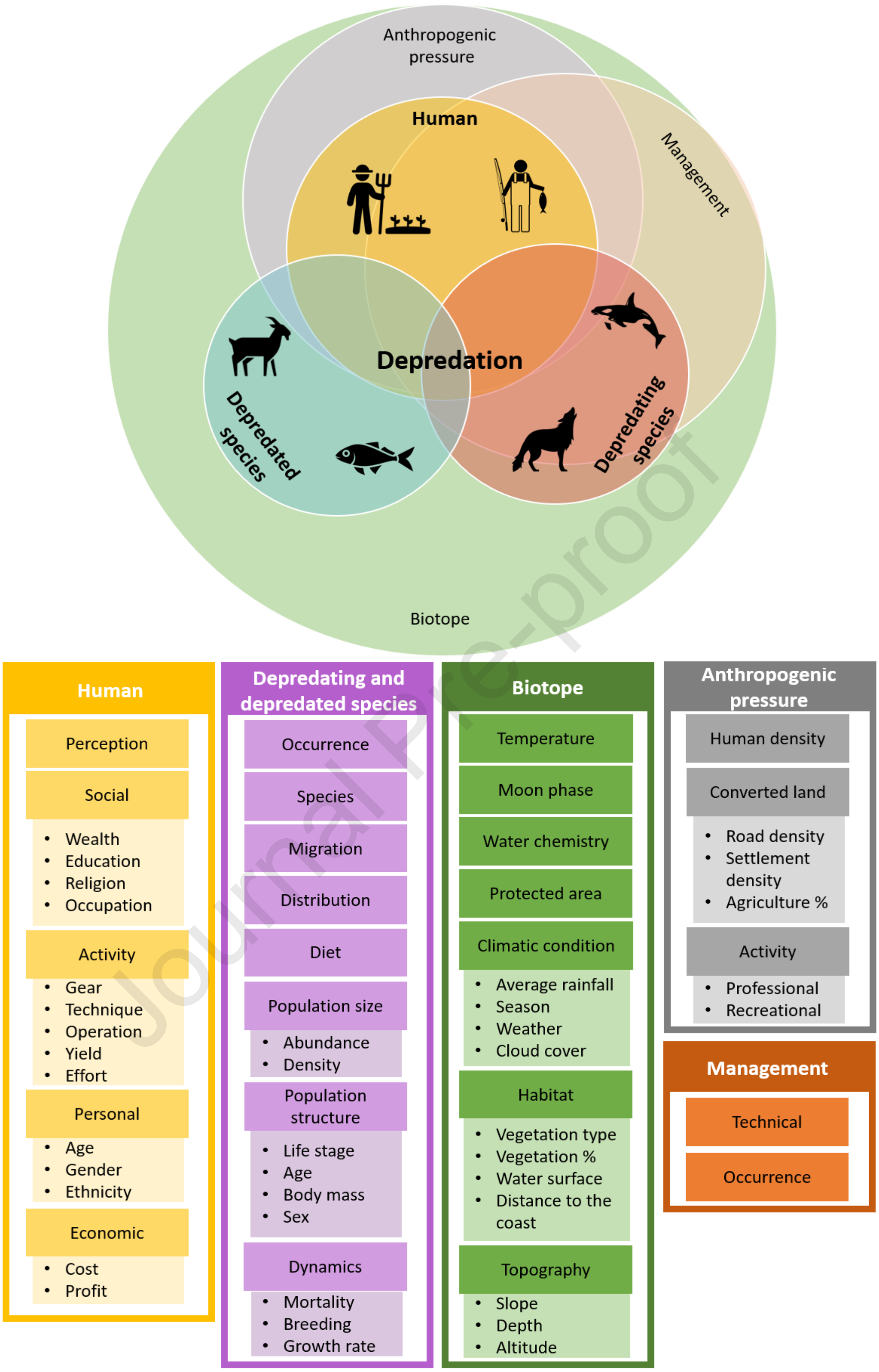


Figure 1: Conceptual diagram of system components in depredation modelling studies. The three main components are humans, depredating species and depredated species. Additional components include biotope, anthropogenic pressure and management. Variables describing each component which were encountered in the reviewed publications are listed in boxes.

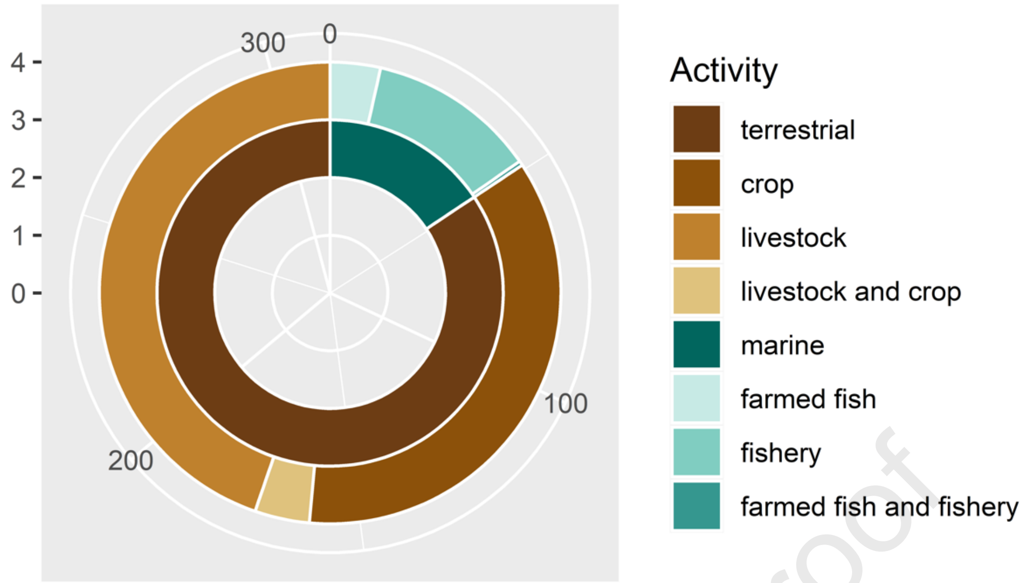


Figure 2: Distribution of the number of reviewed studies using modelling to address depredation per realm (terrestrial or marine) and per human activity subject to depredation.

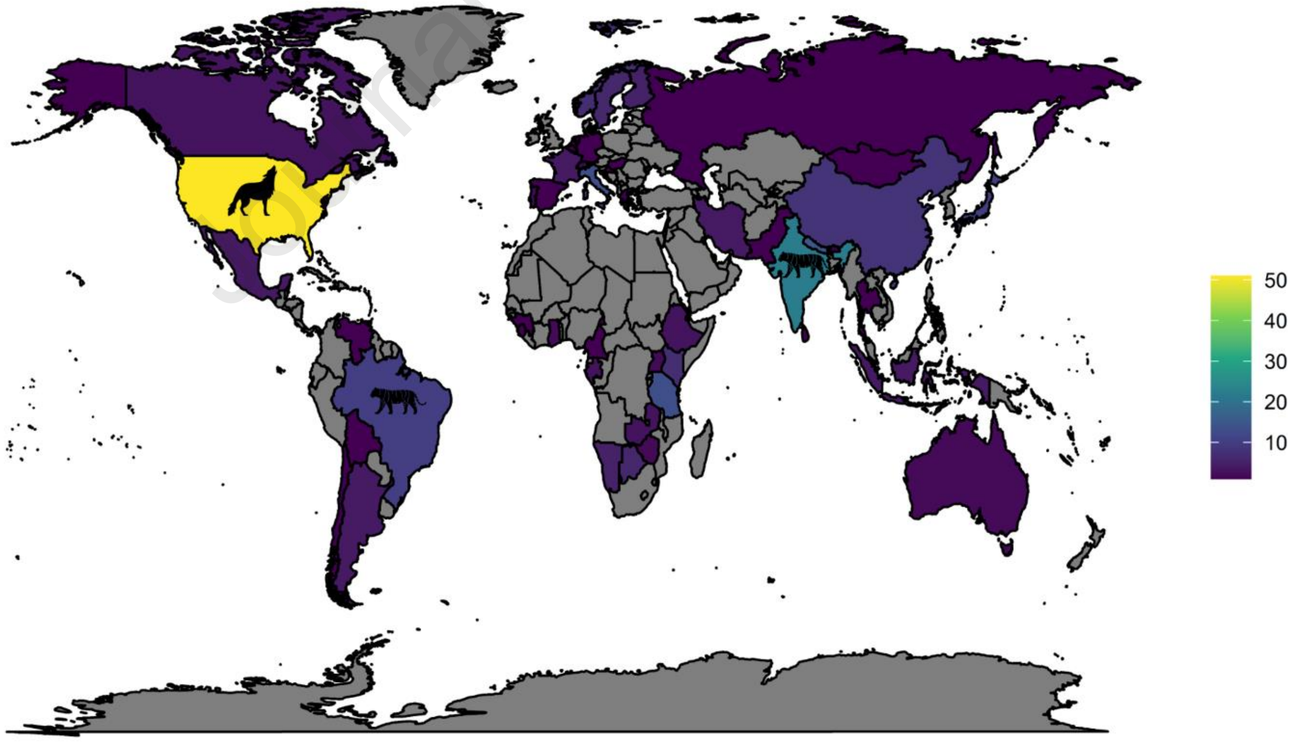


Figure 3: Geographic distribution of the number of reviewed studies using modelling to address depredation in the terrestrial realm summarised by country. Pictograms represent dominant depredating taxa (wolf, big cat) per country.

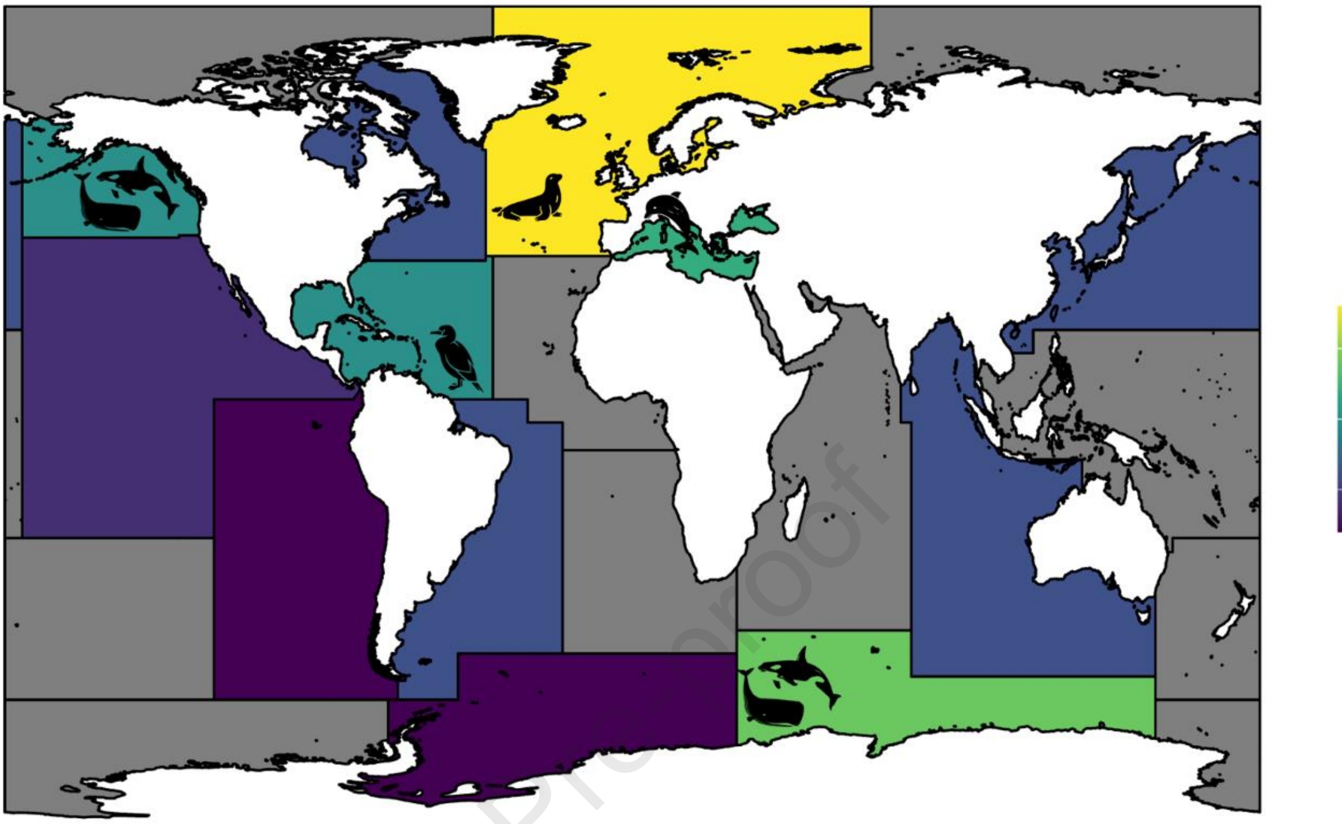


Figure 4: Geographic distribution of the number of reviewed studies using modelling to address depredation in the marine realm summarised by FAO fishing areas. Pictograms represent dominant depredating taxa (cormorant, seal, sperm whale, orca, dolphin) per area.

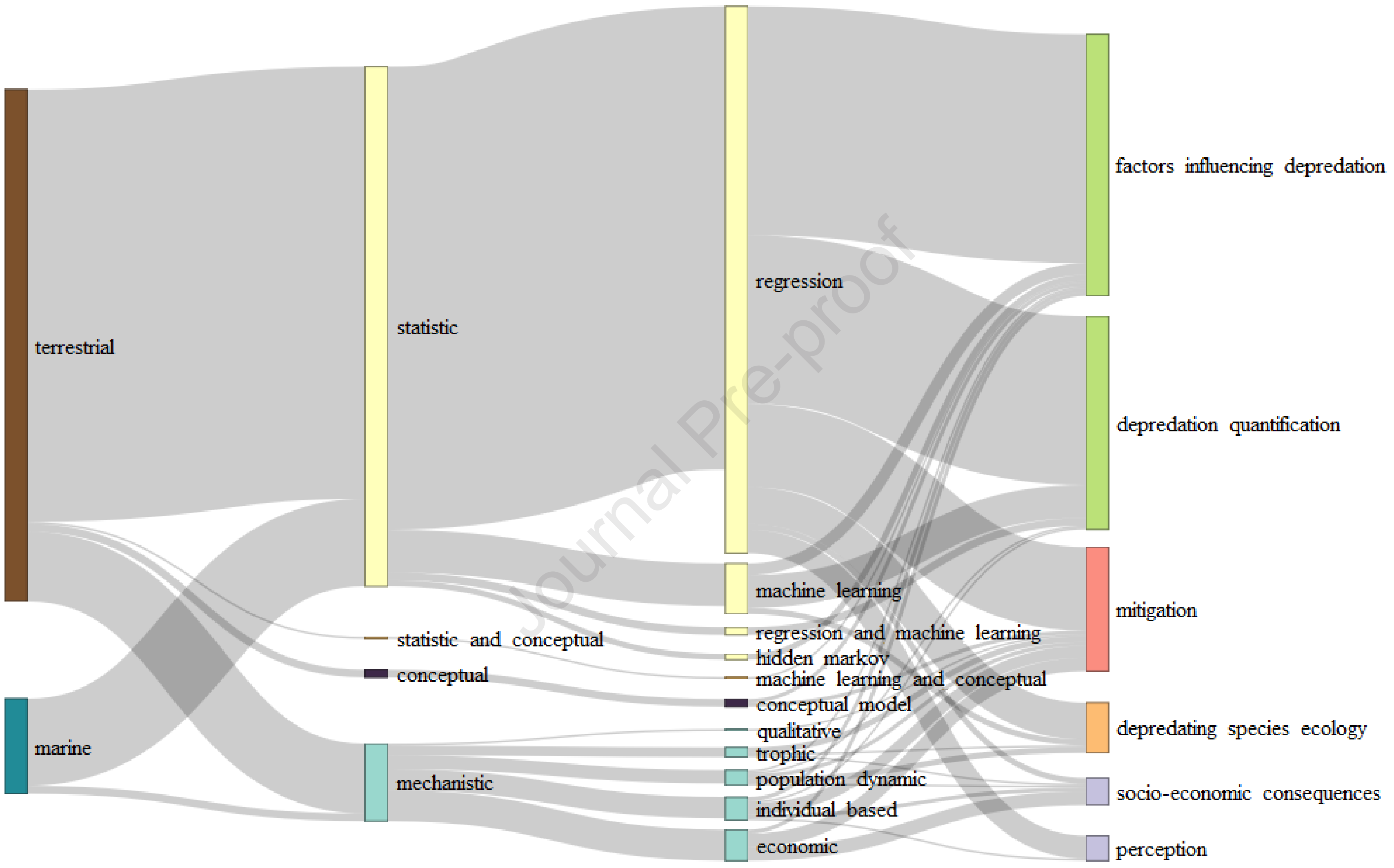


Figure 5: Classification of the reviewed studies using modelling to address depredation according to modelling approach and study purpose.

Figure 6: Percentage of reviewed depredation modelling publications that include specific variables related to each of the three main system components (i.e. depredating species, depredated species and humans). Colour codes indicate how percentages relate either to the number of reviewed papers per realm (i.e., 263 terrestrial studies (brown) and 49 marine studies (blue)), or overall (312 publications (black)).

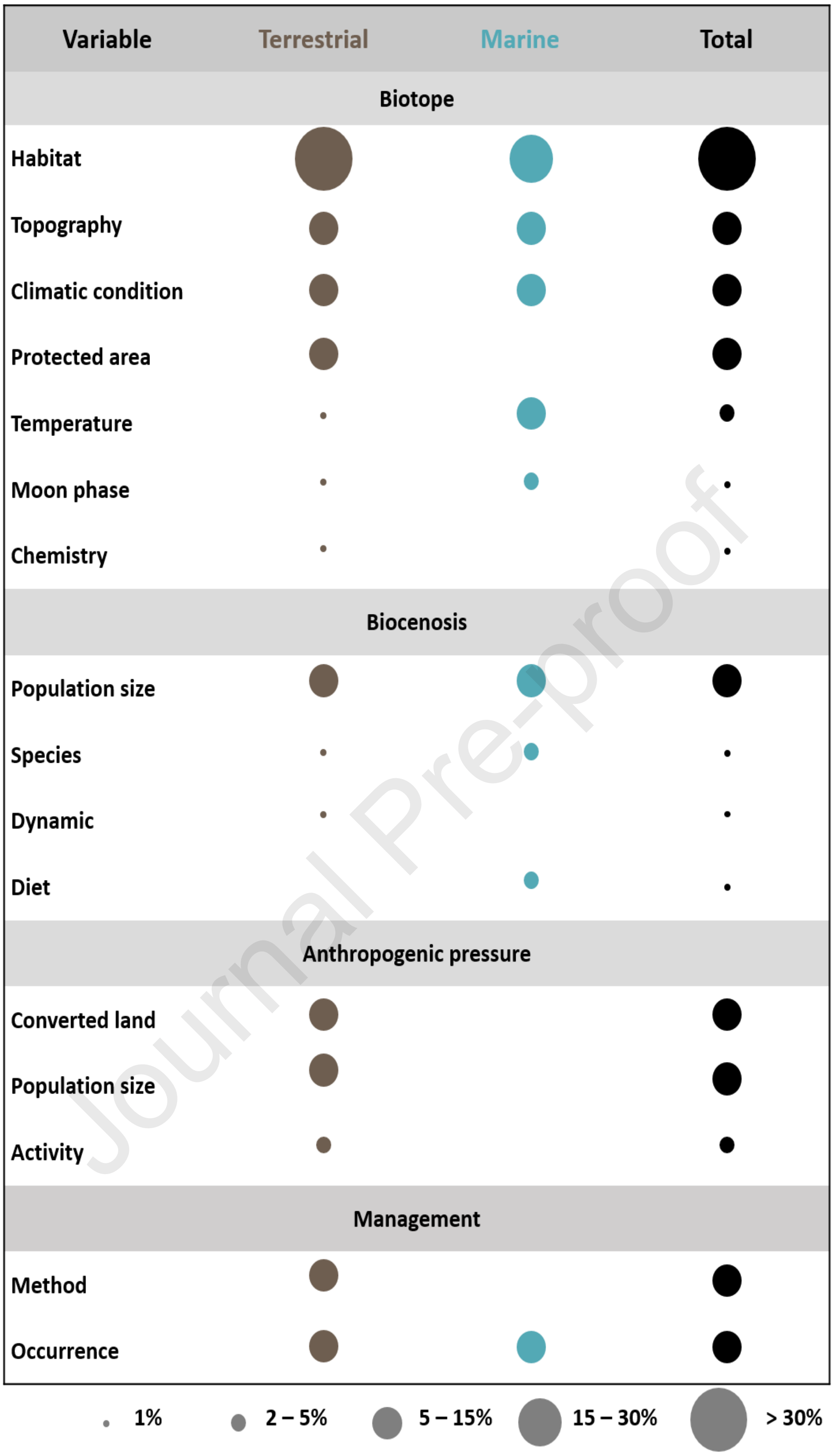


Figure 7: Percentage of reviewed depredation modelling publications including variables describing additional system components, namely: environmental conditions, interacting species community, anthropogenic pressure and management. Colours indicate whether percentages relate to the number of reviewed publications in terrestrial (brown) or marine (blue) realms, or overall (black).

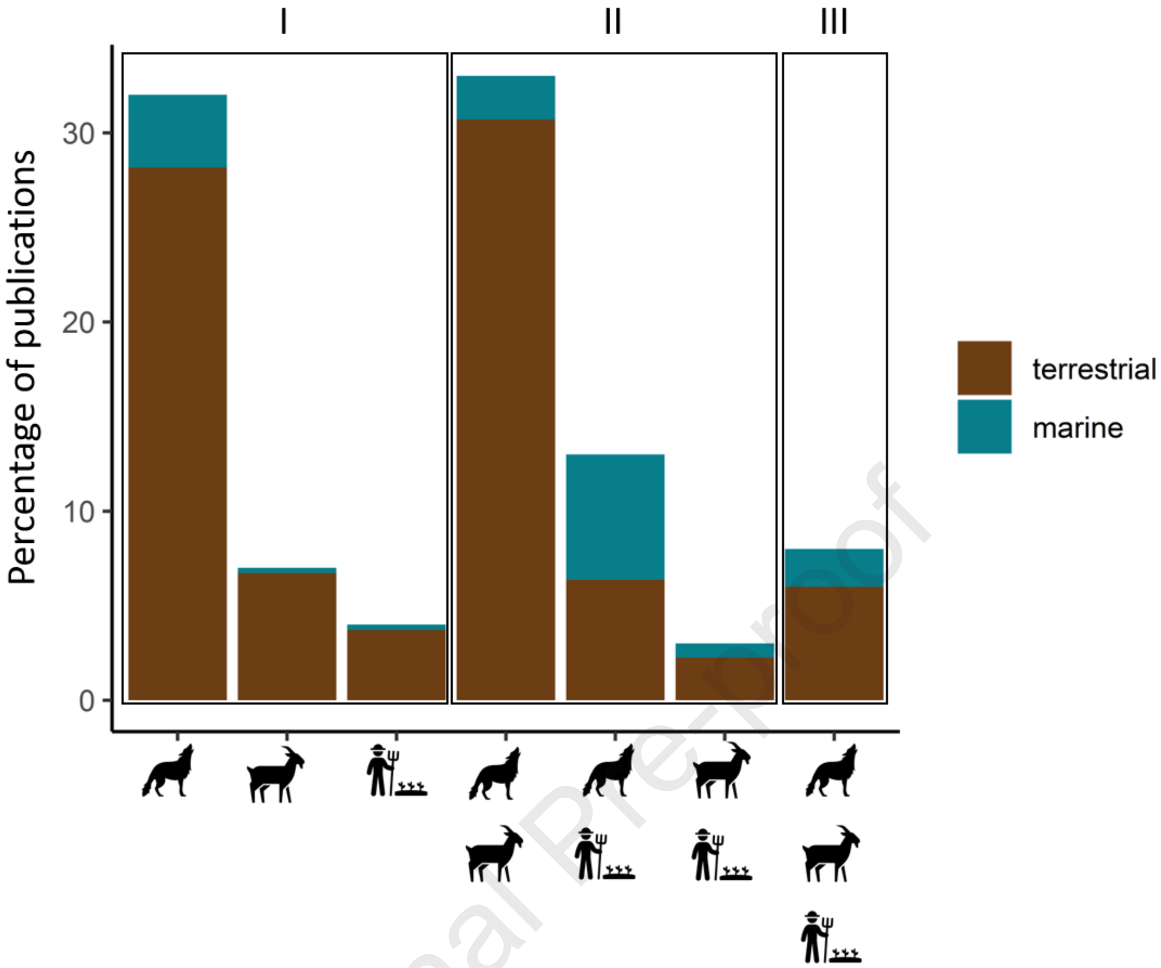


Figure 8: Percentage of reviewed depredation modelling publications including one (I), two (II) or three (III) system components, namely: humans as illustrated by the farmer icon, depredating species as illustrated by the wolf icon or depredated species as illustrated by the goat icon. Colours distinguish between studies in terrestrial (brown) or marine (blue) realms.

Supplementary materials :

Review of depredation modelling across terrestrial and marine realms: state of the art and research needs

Appendix A : Evolution of depredation modelling over time

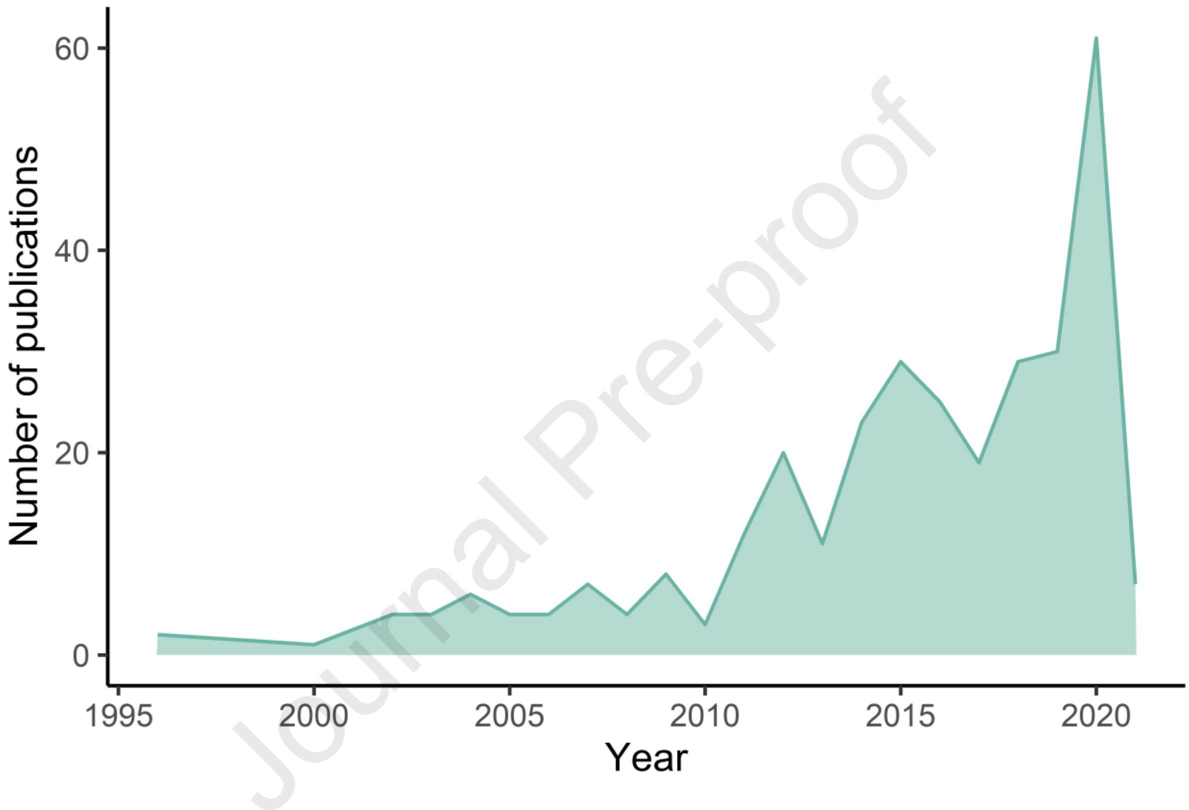
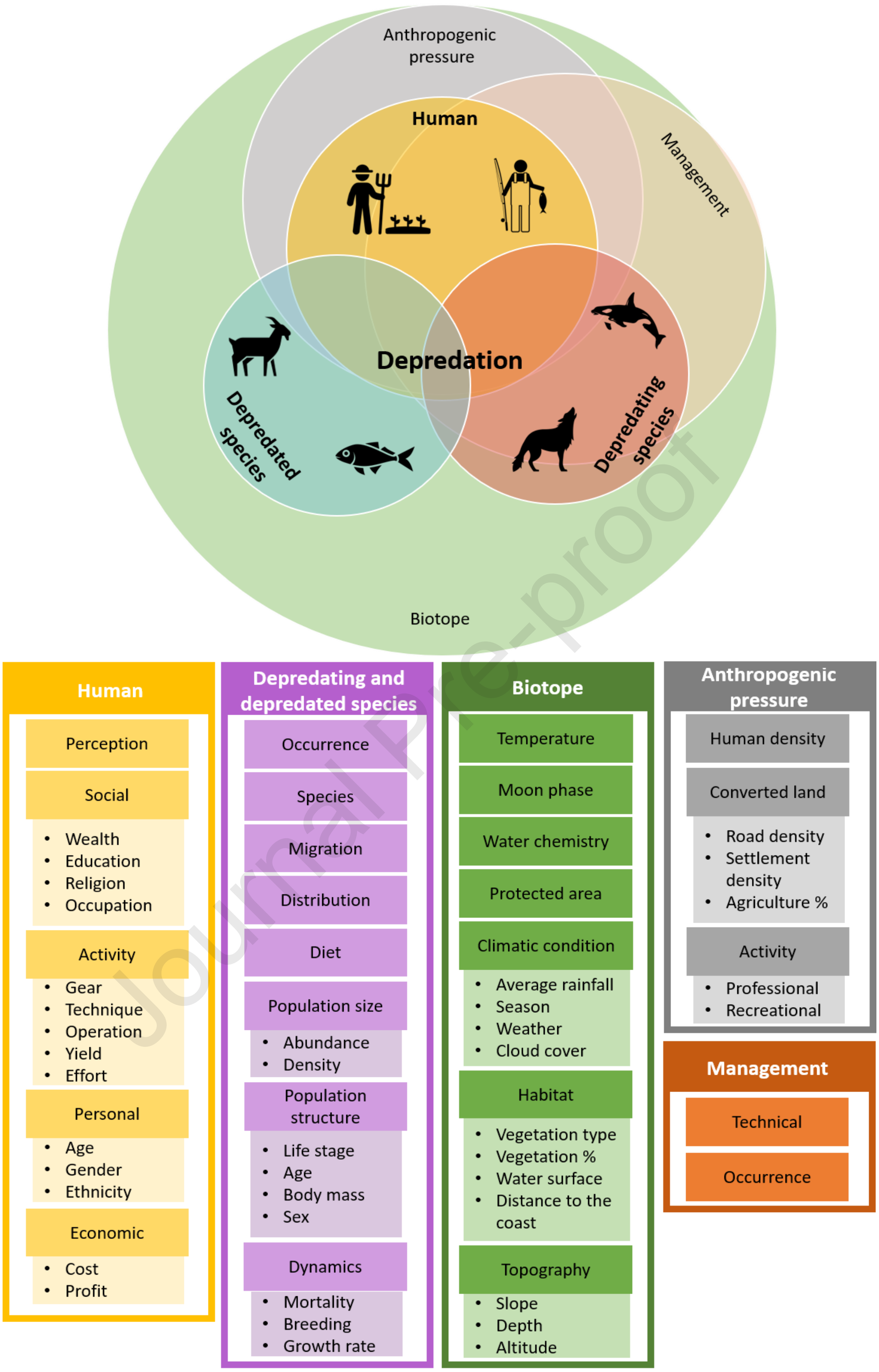


Figure A1: Number of publications addressing depredation using modelling approaches between 1996 and April 2021 (source: Web of Science).

Appendix B :

Table B1. Paper scoring sheet according to targeted categories (in columns). Each line corresponds to a paper.

Requires a link to the data (submitted alongside the manuscript).



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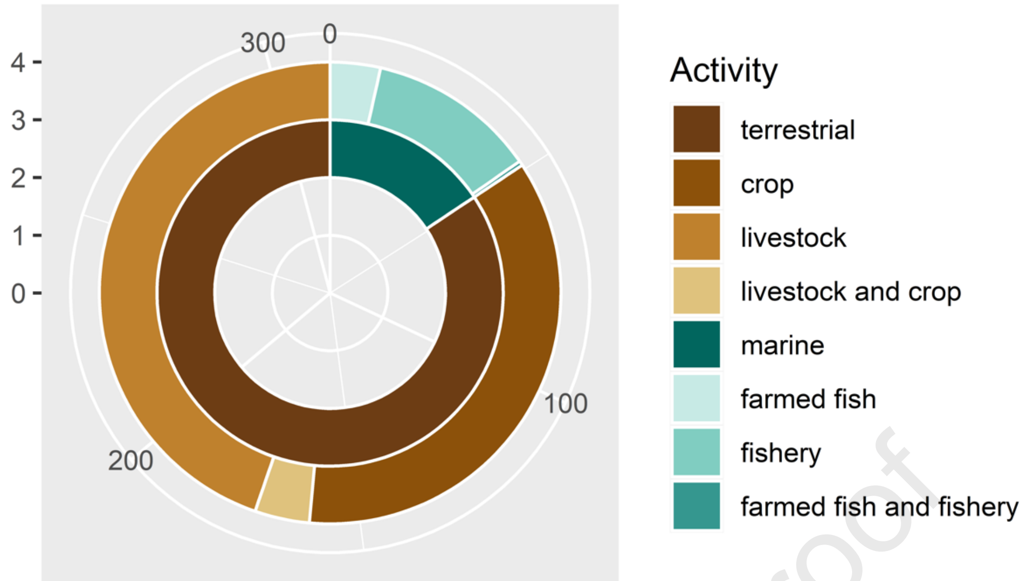

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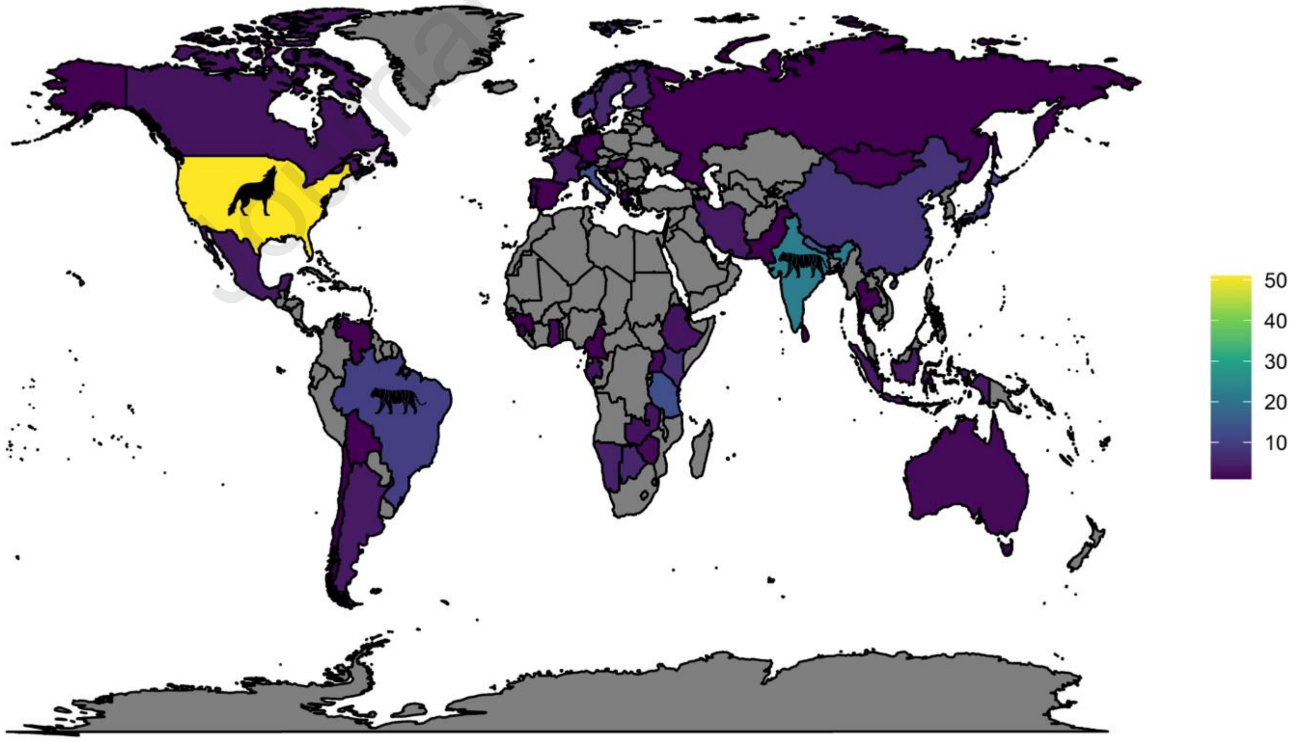

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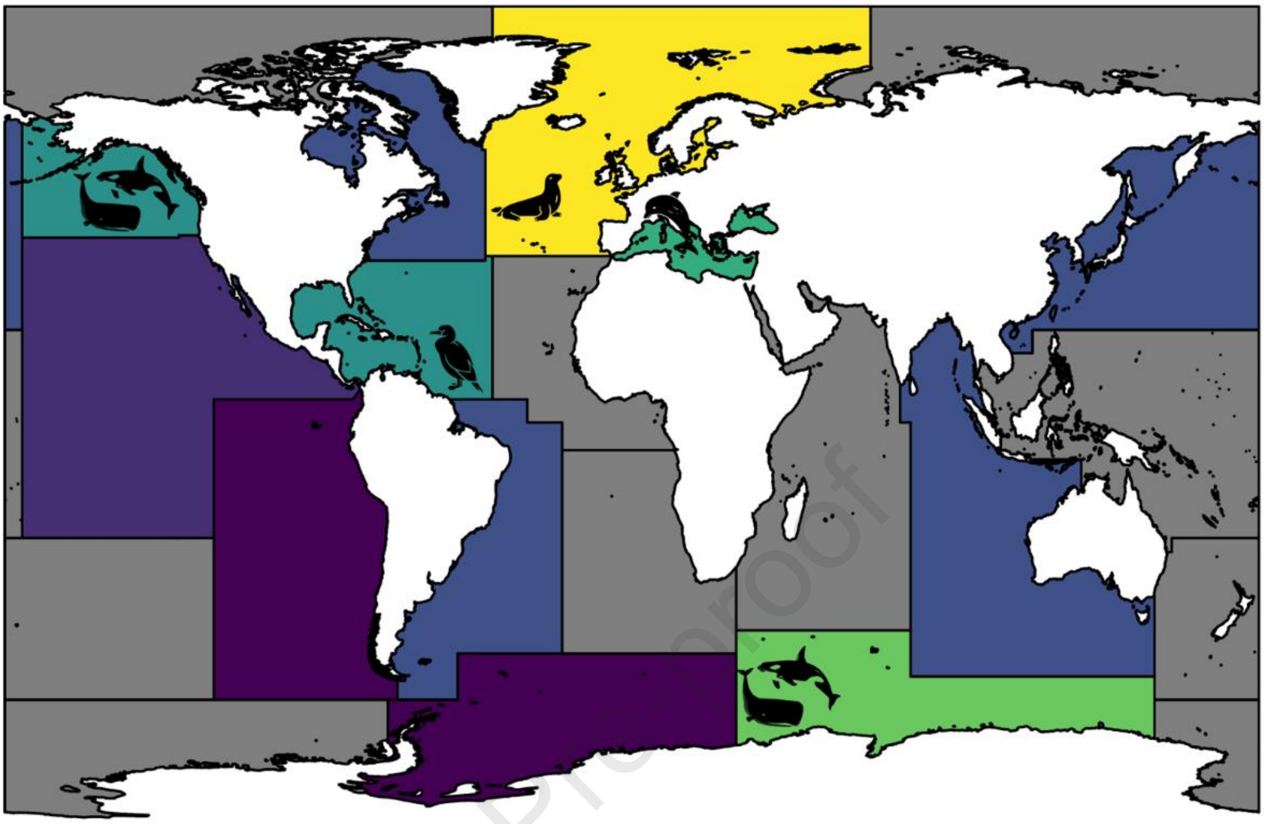

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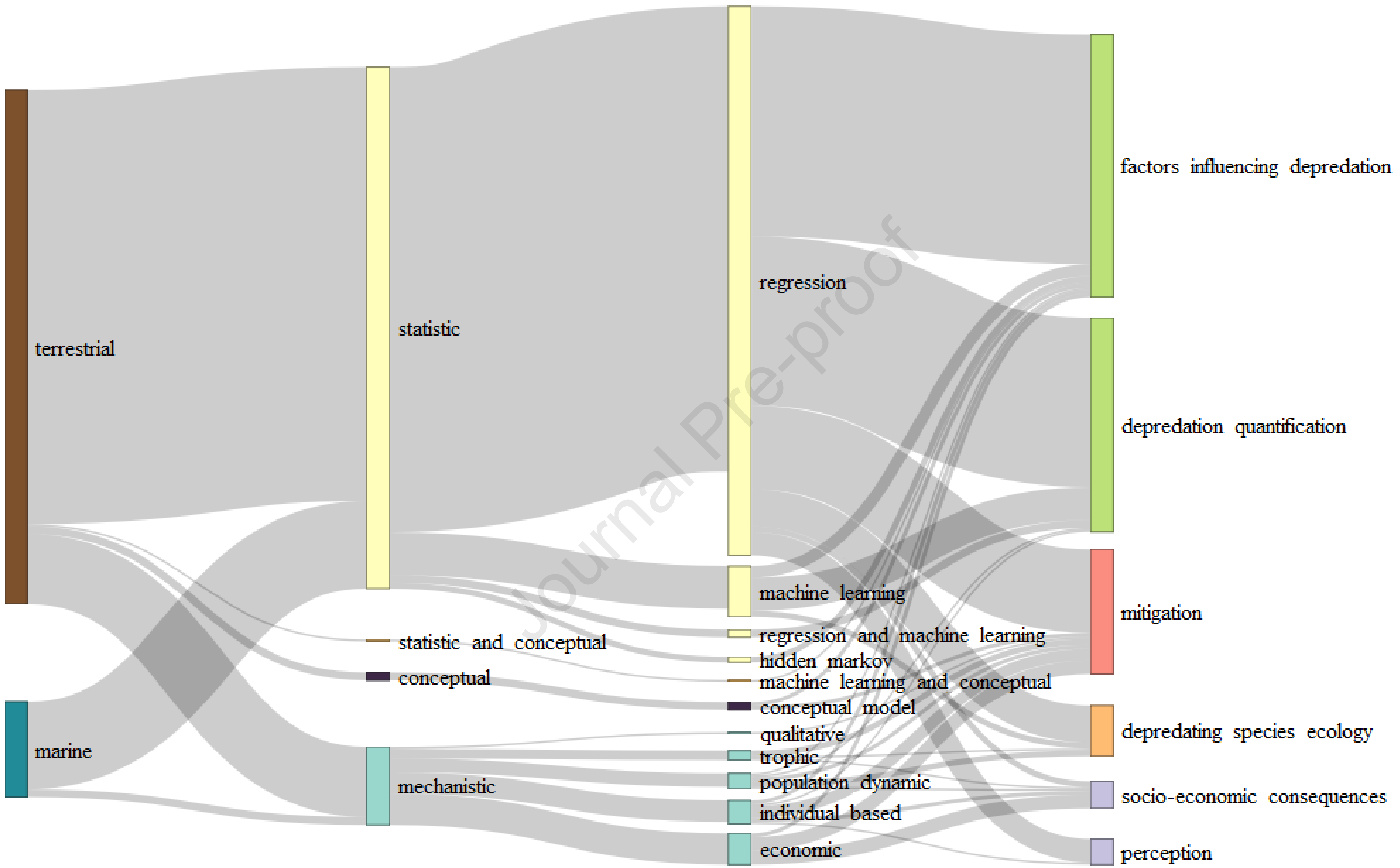

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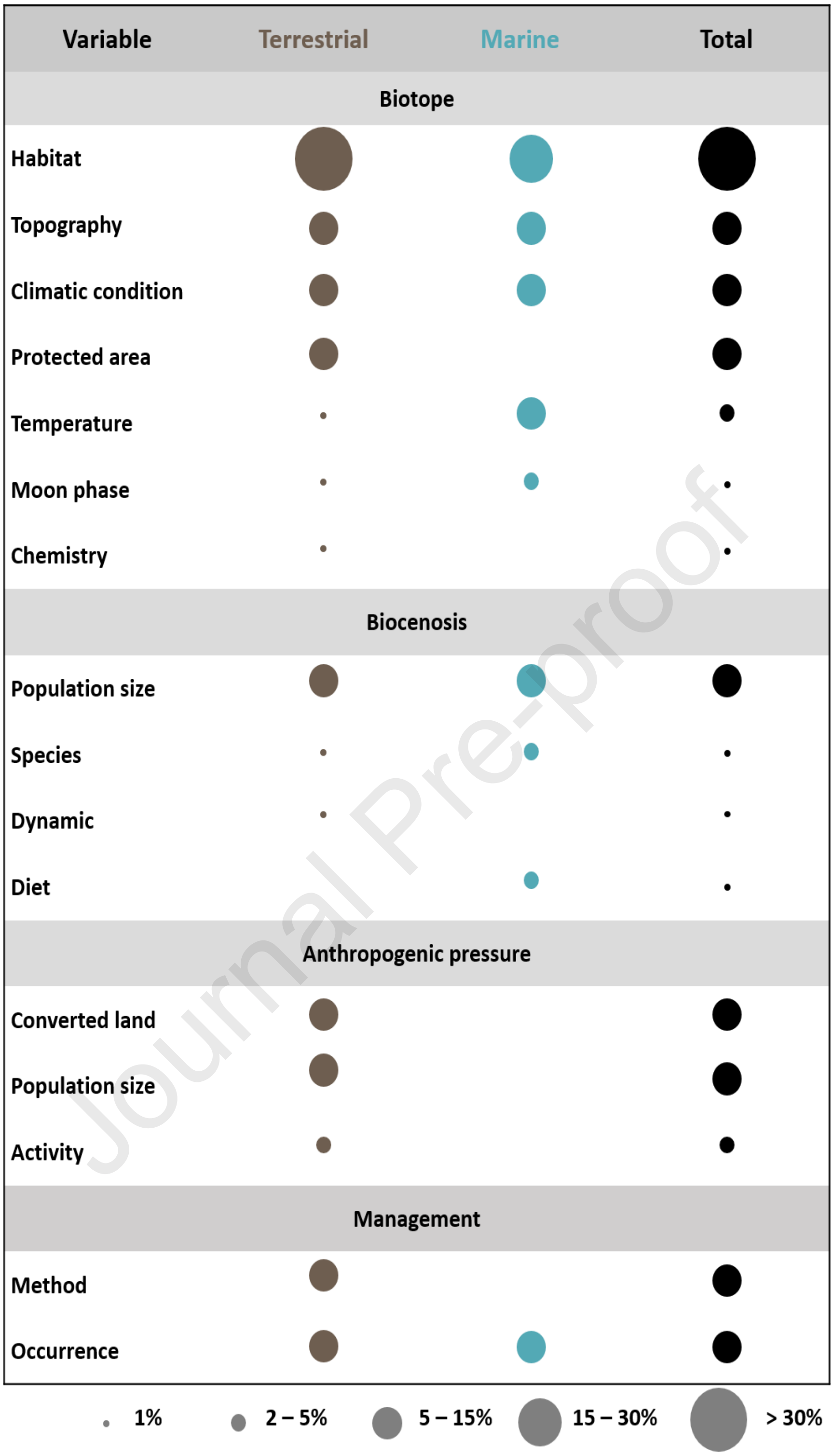

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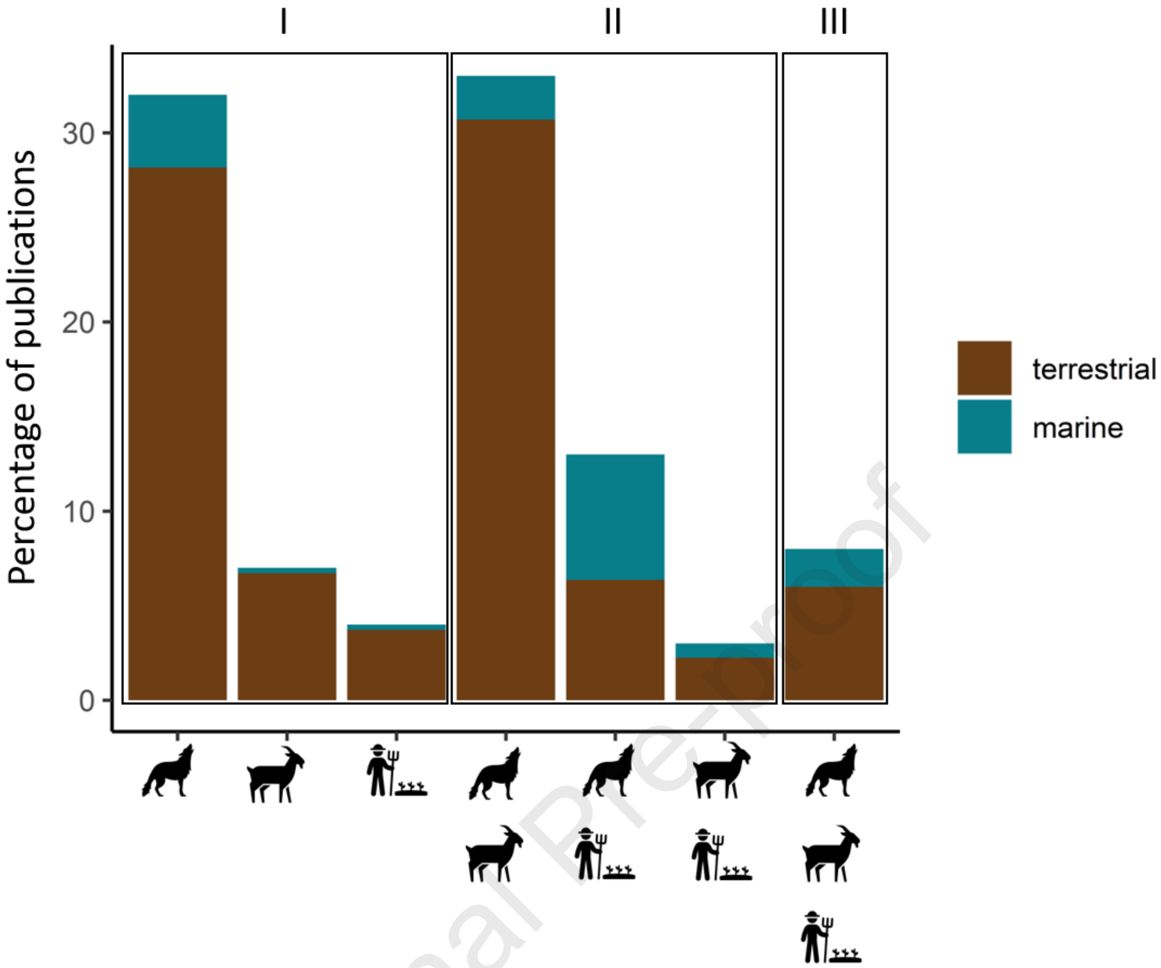

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- We carried out a systematic review to identify relevant approaches to study specific aspects of depredation through modelling
- We identified a numerous statistical models compared with other modelling approaches.
- We identified the main factors driving modelling efforts in the specific case of depredation
- We suggested a number of recommendations for effective depredation modelling
- We highlighted future research priorities to comprehensively model depredation and inform the management of human-wildlife conflicts

Declaration of Interest statement

The authors declare that they have no known competing financial interests or personal relationships that might appear to influence the work reported in the paper entitled: "**A Review of depredation modelling across terrestrial and marine realms: state of the art and future dections**" for publication as a review article in *Environmental Modelling and Software* journal.