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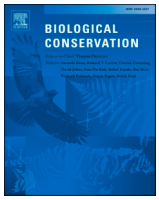

Review

A systematic map of human-carnivore coexistence

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ABSTRACT

Carnivore populations globally have largely declined, and coexistence, where humans and carnivores share landscapes, plays a crucial role in carnivore conservation. However, the term "coexistence" is often used in scientific and popular literature without being clearly defined. Herein, we provide a global perspective on what coexistence is and how it is studied. We conducted a systematic map of 366 articles published between 1987 and 2020 to characterize human-carnivore coexistence literature according to coexistence definitions, temporal trends, geographic and taxonomic focus, and four thematic aspects of coexistence: carnivore ecology, human endeavors, social conflict and human-carnivore conflict. We used chi-squared tests and generalized linear models to describe the thematic, taxonomic and geographic focus of the literature. The human-carnivore coexistence literature increased exponentially in the past 30 years, but few articles defined the term "coexistence" and those that did used inconsistent definitions. Thematically, coexistence research showed less emphasis on social conflict, even though it is a major driver of conflict regarding carnivores. The literature also focused primarily on larger carnivores, rather than endangered carnivores, and was primarily led by European and North American authors. We offer a simplified, formal definition of "coexistence" that incorporates the four thematic aspects of coexistence encountered in the literature: *Co-occurrence of sustainable carnivore populations and human endeavors with minimal human-carnivore and human-human conflict.* We encourage researchers to focus on the social dimensions of coexistence, such as human attitudes towards carnivores or the underlying causes of social conflict, and to broaden the taxonomic and cultural breadth of their projects.

1. Introduction

Carnivore populations globally have largely declined (Dickman et al., 2011; Ripple et al., 2014; Wolf and Ripple, 2017) following similar trends of mammals worldwide (Ceballos and Ehrlich, 2002). Carnivores face myriad conservation challenges. At the top of food webs, they experience large energetic constraints, long generation times and naturally low population densities (Ripple et al., 2014). Additionally, large home ranges often bring them into landscapes with humans, where they predate on livestock, compete for game, or directly attack pets or people (Chapron and Lopez-Bao, 2016; Treves and Karanth, 2003). Where considered threats to human safety and wellbeing, carnivores often face persecution, resulting in dramatic population declines (Bruskotter et al., 2017). Today, 26% of carnivore species are listed as either vulnerable, endangered, or critically endangered by the International Union for the Conservation of Nature (IUCN Red list, 2020).

A primary conservation challenge is to address the need for landscapes that are large enough to sustain viable carnivore populations, while maintaining low levels of conflict with humans. At a local scale, two strategies exist: the separation model, drawing from the concept of remote wilderness, in which wildlife is preserved in protected areas (Packer et al., 2013), and coexistence, in which humans and carnivores share the same landscapes (Carter and Linnell, 2016; Chapron et al., 2014; Harihar et al., 2015; Lute and Carter, 2020). The separation model has proven successful for some large carnivores, such as African lions (*Panthera leo*) in Serengeti National Park in Tanzania (Packer et al., 2013) and wolves (*Canis lupus*) in Yellowstone National Park (Smith et al., 2010; Wuerthner, 2015). However, because reserves can be insufficient in size and connectivity, the human-dominated matrix adjacent to protected areas becomes increasingly important for carnivore conservation, despite potential conflict. For example, lynx (*Lynx lynx*) population distribution is not generally linked to protected areas in Central Europe (Lopez-Bao et al., 2015); black bear density (*Ursus americanus*) is three times higher in urban areas than in natural areas in

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North America (Beckmann and Berger, 2003); spotted hyena (*Crocuta crocuta*) abundance is 15 times higher around human settlements than in natural areas in Ethiopia (Yirga et al., 2015); and agricultural lands support populations of leopards (*Panthera pardus*), striped hyenas (*Hyena hyena*) and Indian gray wolves (*Canis lupus pallipes*) in western India (Majgaonkar et al., 2019). Often, human encroachment into carnivore ranges has already led to co-occurrence, making it indispensable to start considering carnivores as a part of socio-ecological systems where the well-being of people and predators is mutually dependent (Exposito-Granados et al., 2019). Moreover, sharing space and coexisting with carnivores might help people recognize these predators as legitimate occupants of human-dominated landscapes, benefiting carnivore conservation (Lopez-Bao et al., 2017; Pooley, 2021).

When humans and carnivores share landscapes and conflict occurs, diverse stakeholders often have strong opinions about living with carnivores and debate over conflict management (Niemiec et al., 2020). Goals and attitudes differ among stakeholders, frequently linked to underlying social conflict (Madden and McQuinn, 2014). In this context, agreeing on the meaning of the terms used to define objectives, like coexistence, is indispensable for constructive dialogue and decision-making, as well as to efficiently measure success of conservation efforts. The term "coexistence" is often used in both scientific and popular literature without being clearly defined (Carter and Linnell, 2016; Knox et al., 2021; Lute and Carter, 2020). While some have published their own framework for coexistence (Carter and Linnell, 2016; Chapron and Lopez-Bao, 2016; Frank and Glikman, 2019; Pooley, 2021), it remains unclear what definitions are accepted and used by researchers and practitioners (Glikman et al., 2021).

In this study, our goal was to conduct a systematic map of the scientific literature on human-carnivore coexistence, providing a global perspective on what coexistence is and how it is studied. We compiled existing definitions of the term and characterized the systems that foster research about coexistence. We measured the volume of publications studying and defining coexistence, their geographic and taxonomic focus, and the types of conflicts investigated. We predicted that few studies would explicitly define the term "coexistence" (Carter and Linnell, 2016; Lute and Carter, 2020). Although conflicts impact both human livelihoods and carnivores, we also expected that outcomes affecting humans, specifically human food such as livestock, would draw particular attention (Exposito-Granados et al., 2019; Lozano et al., 2019; Torres et al., 2018). Further, because the concept of coexistence emerges from the need to mitigate conflicts, we expected coexistence research to be predominantly motivated by human-carnivore conflict, more so than social conflict among stakeholder groups (Exposito-Granados et al., 2019; Lozano et al., 2019). We also predicted that research about coexistence would focus on large, carnivorous, and threatened carnivores because they are considered charismatic, dangerous, or worthy of conservation focus (Albert et al., 2018; Johnson et al., 2010; Martin-Lopez et al., 2008). Finally, we expected research efforts to be geographically biased, towards countries with better capacity to fund research and publish in international journals (Lozano et al., 2019) or towards regions with high densities of humans and carnivores and thus hotspots of conflict (Boomgaard, 2010).

2. Materials and methods

2.1. Search and eligibility screening

We followed guidelines for systematic maps by the Collaboration for Environmental Evidence (2018). Systematic maps are a method to collect, code and configure evidence relating to a specific subject. We designed the search to include all English-language scientific articles that are indexed by the Web of Science database and deal with human-carnivore coexistence. We developed a search string that would yield all articles mentioning any form of the term "coexistence" associated with either the term "carnivore" or a genus of the order Carnivora in their title, abstract, keywords, or Web of Science KeywordsPlus; reference to carnivores could be either Latin scientific or English common names (see Appendix A for the full search string). We recognize that some studies investigating human-carnivore conflict might not have used the term "coexistence" but rather related terms such as "conflict mitigation", "co-occurrence", "co-adaptation", "co-inhabiting", or "land-sharing" (Kshettry et al., 2020). Such articles were not yielded by this search string. Thus, our results focus on studies that use the term "coexistence" explicitly, rather than the study of coexistence as a general theme in the scientific literature.

We performed the search on the Web of Science Core Collection database, through an access granted by Clarivate Analytics, on February 3, 2020. Therefore, our search results are dependent on the coverage of the Web of Science Core Collection. The search yielded 5131 articles published between 1900 and 2020. We removed the two identical duplicates identified in EndNote X9 and exported the remaining articles in the Rayyan QCRI web-tool. Articles were then screened for eligibility following a two-step process. During the first phase, we reviewed titles and abstracts and excluded articles that were not in English, or in which search terms were used in the wrong context (see Appendix B for details on the screening process). For example, many articles were excluded due to the homonymity of search terms (e.g., "bear", "seal", "genet") or because they studied coexistence between species different from humans and mammalian carnivores. Humans could be referred to by human groups, activities or properties (e.g., "local communities", "husbandry practices", "fisheries", "urban areas", "domestic animals"). We included all peer-reviewed articles (empirical studies, reviews, conceptual articles, models, book chapters) because authors might propose a definition for coexistence in any of these article types and because the total volume of such peer-reviewed articles is indicative of the scientific interest in the topic.

During the second phase, we reviewed the full content of included articles (excluding supplementary material) following the same exclusion criteria. We further excluded articles yielded by the KeywordsPlus algorithm if the term "coexistence" was present in the cited literature but never mentioned by the authors in their full text (see Appendix B). This process led to a final number of 366 articles.

2.2. Data coding

We recorded general characteristics of each article, including title, authors, abstract, journal and year of publication. Since our coding varied among types of articles, we also recorded whether the article was empirical (including empirical studies, modelling papers and systematic reviews) or conceptual (including essays, qualitative reviews and book chapters). We recorded if empirical articles collected, measured, modelled, or analyzed data and if conceptual articles discussed data (hereafter "studied"). We also extracted data on: (1) geography of the study area(s), including country and continent; (2) whether the land use of the study area(s) was urban and/or rural, following study site description by author(s) or, if unavailable, urban-rural classification by the United States Census Bureau (U.S. Census Bureau, 2020); and (3) country of residency of the lead author. We also collected data on taxonomic focus of the study, including species of the *Homo* genus (*Homo sapiens*, *Homo neanderthalensis*, or *Homo antecessor*) and Carnivora species and families (comprising 18 families of the Carnivora order: Ailuridae, Amphicyonidae, Canidae, Eupleridae, Felidae, Herpestidae, Hyaenidae, Mephitidae, Mustelidae, Nandiniidae, Nimravidae, Odobenidae, Otariidae, Phocidae, Prionodontidae, Procyonidae, Ursidae and Viverridae).

Finally, we recorded whether the article explicitly defined the term "coexistence" or referred to four thematic aspects of the concept of coexistence identified prior to the coding: (1) *carnivore ecology*, studied at the individual, population, community, or ecosystem levels; (2) *human endeavors*, defined as human activities aiming to achieve goals,

such as economic prosperity or fulfillment in life; (3) *social conflict* among stakeholder groups regarding carnivores, defined as a "struggle over values or claims to status, power, and scarce resources, in which the aims of the conflict groups are not only to gain the desired values, but also to neutralize, injure, or eliminate rivals" (Oberschall, 1978); and (4) *human-carnivore conflicts*, defined as negative impacts to humans or carnivores resulting from their direct interactions. To assess whether an article referred to *carnivore ecology*, we recorded if it collected empirical data on carnivores at any of the levels mentioned above (e.g., studies of carnivore physiology, behavior, demography, community interactions). To assess whether an article referred to *human endeavors*, we recorded whether it studied human dimensions, including cultural, demographic, ecological, economic, geographical, historical, paleontological, psychological, or sociological approaches. Examples of *human endeavors* included agricultural livelihoods, hunting, recreational activities, and feelings of personal safety when co-occurring with carnivores. Additionally, we assessed specifically whether an article studied human knowledge, values, beliefs, perceptions, or attitudes towards carnivores (labeled "human attitudes"), and whether it studied the economic impact of carnivores on people, including cost or need of compensation. For *social conflict*, we assessed whether articles reported any disagreements among stakeholders over issues related to carnivores (e.g., social science data showing disparities in attitudes towards carnivores). For *human-carnivore conflicts*, we assessed if an article reported negative impacts on humans or carnivores resulting from their direct interactions. Impacts to humans included separate categories for threats to human safety (e.g., direct attack or disease transmission), human property (e.g., damage to buildings, vehicles, garbage dumpsters, or fishing nets), pets (e.g., direct attack or disease transmission), livestock (e.g., direct attack or disease transmission), game (e.g., predation by carnivores), fish stocks (e.g., predation by carnivores), and other agriculture (e.g., beehives, crops, poultry). Impacts to carnivores could be at the individual, population, or community levels and included separate categories for demographic impacts (e.g., survival or mortality rate, reproduction rate, population size, population viability), non-demographic impacts (e.g., genetics, diet, behavior, space use, and intra- or interspecific interactions), intentional killing (including legal and illegal), accidental deaths (e.g., road kills), translocations (e.g., relocations and non-lethal removal of problematic individuals), and disease (transferred from humans or domestic animals).

2.3. Analysis

To identify temporal trends of the coexistence literature, we calculated the annual publication volume of coexistence literature and compared it to the total publication volume in the journals used in this systematic map. Although we used all 366 articles for the rest of the analyses, we excluded the one journal article published in 2020 (through the February 3rd search date) from the temporal analysis to allow for consistent annual comparisons. We also excluded book chapters (n = 12) from the temporal analysis because they were only published once and did not occur in journals published annually. Thus, 353 journal articles were retained for temporal analyses. We then extracted the list of journals (n = 141) that published at least one of the 353 articles and their annual publication volume indexed in Web of Science, available between 1997 and 2019 (Clarivate Analytics, 2020). We then calculated the ratio of journal articles about coexistence over total annual publication volume of the 141 journals.

To characterize the thematic focus of coexistence research, we calculated the total number of articles studying at least one of the four identified thematic aspects of coexistence: *carnivore ecology*, *human endeavors*, *social conflict* and *human-carnivore conflict*. An article studying two or more of these themes was counted separately in each theme. To determine if there were statistical differences in the number of articles within each theme, we performed McNemar's chi-squared test for each pair of themes, with Bonferroni's correction for multiple comparisons.

To further characterize the thematic emphasis of coexistence research, we quantified the number of articles studying each of the following subcategories: (1) carnivore populations (e.g., survival or mortality rate, reproduction rate, population size, population viability; part of the *carnivore ecology* theme); (2) human attitudes (e.g., social science data on human knowledge, values, beliefs, perceptions, or attitudes towards carnivores; part of the *human endeavors* theme); (3) economic impact of carnivores on human livelihoods (e.g., estimates of the economic cost of carnivores on humans or the need of financial compensation; part of the *human endeavors* theme); and human-carnivore conflicts (4) impacting humans and (5) impacting carnivores (part of the *human-carnivore conflict* theme). We calculated the total number of articles studying each type of human-carnivore conflict and performed a chi-squared goodness of fit to test if frequencies significantly varied across conflict types.

To evaluate taxonomic research focus, we compared the number of publications focused on each coded Carnivora family. We used a chi-squared goodness of fit to test if frequencies significantly varied across families. We also calculated the total number of articles focusing on each of the 296 species of carnivores listed by the IUCN Red list (2020). This excluded 10 species initially present in the data: 3 domestic species (*Felis catus, Canis familiaris* and *Canis dingo)* and 7 extinct species (*Canis mosbachensis, Vulpes praeglacialis, Homotherium latidens, Smilodon populator, Mustela palermina, Ailuropoda baconi,* and *Arctodus simus*). In order to test the hypothesis that coexistence research would be biased towards large, carnivorous or endangered species, we used Gittleman's (1985) list of carnivore body mass and diet and the IUCN conservation status (IUCN Red list, 2020). Diets included 5 categories: 'carnivorous', 'herbivorous', 'omnivorous', 'piscivore' and 'insectivorous'. Conservation status included 7 categories: 'extinct', 'critically endangered', 'endangered', 'vulnerable', 'near threatened', 'least concern' and 'data deficient'. We used a generalized linear model with a quasi-Poisson distribution and a log link function to test which variables explained the taxonomic focus of coexistence research. Generalized linear models and Poisson distributions account well for count data that do not follow the assumptions of linear models. However, data showed evidence of overdispersion, so we used a quasi-Poisson distribution that allows additional free parameters in the model. We also used likelihood ratio tests to assess if publication volume differed for body mass, diet and conservation status across focal carnivore species. To further characterize the effect of diet on publication volume, we estimated the marginal mean publication volume by each category of diet. Tukey's honest significance test was performed to determine which categories were significantly different in publication volume.

We quantified the geographic focus of human-carnivore coexistence research at two levels: continent and country. We compared the publication volume across continents of origin of both the study area and residency of the lead author and used a chi-squared goodness of fit to test if frequencies significantly varied across continents. To test our hypothesis of bias of coexistence research towards countries with better capacities of publishing in international journals, we evaluated the economic development of each country, assuming it reflected opportunities to publish research. We used the Natural Earth dataset (2020) to retrieve each country's level of economic development, which we grouped into four categories: 'developed', 'emerging', 'developing' and 'least developed'. To test the hypothesis of a coexistence research focus on regions with higher human and carnivore densities, we used the most recent human population estimate of each country (Natural Earth, 2020) and most recent estimate of the number of carnivore species present in each country (IUCN Red list, 2020). To test whether economic development, human population and carnivore species richness differed across countries, we used a generalized linear model with a quasi-Poisson distribution and a log link function. Likelihood ratio tests were used to assess if publication volume differed for each variable across study area and lead author country. We also compared the mean publication volume of each category of economic development by

performing Tukey's honest significance test.

Statistical analyses were performed in R version 3.6.2. (R Core Team, 2019), using the car (version 3.0-9) (Fox and Weisberg, 2019), emmeans (version 1.5.1) (Searle et al., 1980) and FactoMineR (version 2.3) (Le et al., 2008) packages to conduct generalized linear models.

3. Results

3.1. Temporal distribution

We included a total of 366 articles, published between 1987 and 2020. 77.9% (n = 285) were coded as empirical studies and 22.1% (n = 81) as conceptual articles. 353 articles published between 1987 and 2019 were retained for temporal analysis. The volume of publications regarding human-carnivore coexistence and the proportion of the total publication volume in journals increased over time, particularly in the last six years (Fig. 1A). This increase of interest in human-carnivore coexistence is mainly led by the study of gray wolves (*C. lupus*) (Fig. 1B), with study areas mostly located in the United States and India (Fig. 1C) and led by authors generally originating from the United States (Fig. 1D).

3.2. Thematic focus

Of 366 articles, only 3.8% (n = 14) defined the term "coexistence"; 2.7% (n = 10) proposed an original definition and 1.1% (n = 4) cited other authors. Of the 4 articles defining coexistence by citing other authors, all cited Carter and Linnell's (2016) definition: '*a dynamic but sustainable state in which humans and large carnivores co-adapt to living in shared landscapes where human interactions with carnivores are governed by effective institutions that ensure long-term carnivore population persistence, social legitimacy, and tolerable levels of risk*'. The 10 original definitions offered various interpretations of the term "coexistence", and only 2 (Carter and Linnell, 2016; Varjopuro, 2011) mentioned social conflict between stakeholders (see Appendix C for a list of the original definitions of human-carnivore coexistence).

Out of 366 articles, 91.3% (n = 334) studied *human endeavors*, 80.6% (n = 295) studied *human-carnivore conflicts*, 71.3% (n = 261) studied *carnivore ecology*, and 30.9% (n = 113) studied *social conflict* (Fig. 2A). 3.6% of articles (n = 13) studied *carnivore ecology* and no other theme. All pairwise combinations of themes differed in publication volume (all McNemar's $\chi^2 > 11.33$; all $p < 0.001$) (see Appendix D for individual test results).

Of the 334 articles studying *human endeavors*, 50.6% (n = 169) studied human attitudes towards carnivores and 21.3% (n = 71) studied the economic impact of carnivores on people. Of the 261 articles studying *carnivore ecology*, 44.4% (n = 116) did so at the population level. Of the 295 articles studying *human-carnivore conflict*, 68.8% (n = 203) studied impacts on carnivores and 66.4% (n = 196) studied impacts on humans, which was not significantly different ($\chi^2 = 0.04$; df = 1; $p = 0.837$). Of the 203 articles studying impacts on carnivores, 60.6% (n = 123) studied non-demographic impacts (e.g., smaller home ranges, increased nocturnal activity, or diet shifts), 50.7% (n = 103) studied intentional killings, 15.8% (n = 32) studied demographic impacts, 11.3% (n = 23) studied accidental deaths, 7.4% (n = 15) studied translocations and 3.0% (n = 6) studied diseases. These proportions differed significantly from an equal distribution among conflicts ($\chi^2 = 120.71$; df = 5; $p < 0.001$) (Fig. 2B). Of the 196 articles studying impacts on humans, 76.0% (n = 149) studied livestock depredation, 37.8% (n = 74) studied threats to human safety, 16.8% (n = 33) studied impacts on agriculture, 15.3% (n = 30) studied impacts on human property, 9.7% (n = 19) studied threats to pets, 7.1% (n = 14) studied impacts on game and 4.6% (n = 9) studied impacts on fish stocks. These proportions differed significantly from an equal distribution among conflicts ($\chi^2 = 162.69$; df = 6; $p < 0.001$) (Fig. 2C).

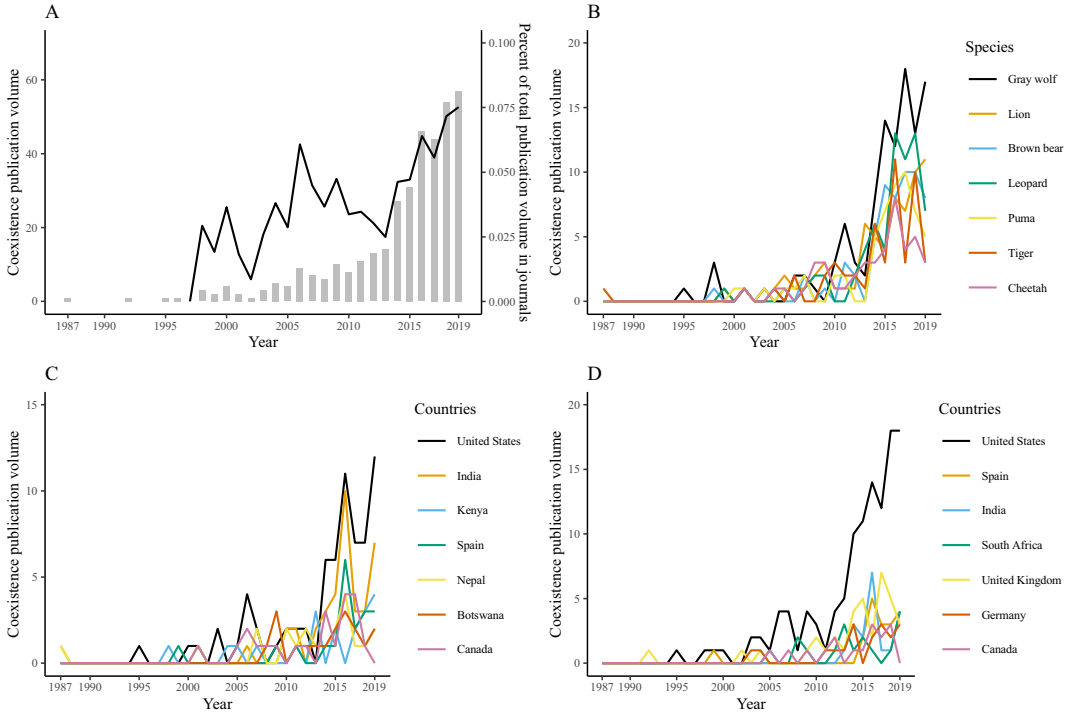

Fig. 1. Temporal distribution of published research about human-carnivore coexistence. (A) The annual publication volume on coexistence is shown as raw numbers by gray bars and as percentage of the total publication volume in journals used in this systematic map (n = 141) by the black line. (B) Annual publication volume for the 7 most studied Carnivora species. (C) Annual publication volume for the 7 most studied countries in terms of study area. (D) Annual publication volume for the 7 most studied countries in terms of residency of lead authors. In (B), (C) and (D), labels are ordered from most to least studied species and countries in 2019.

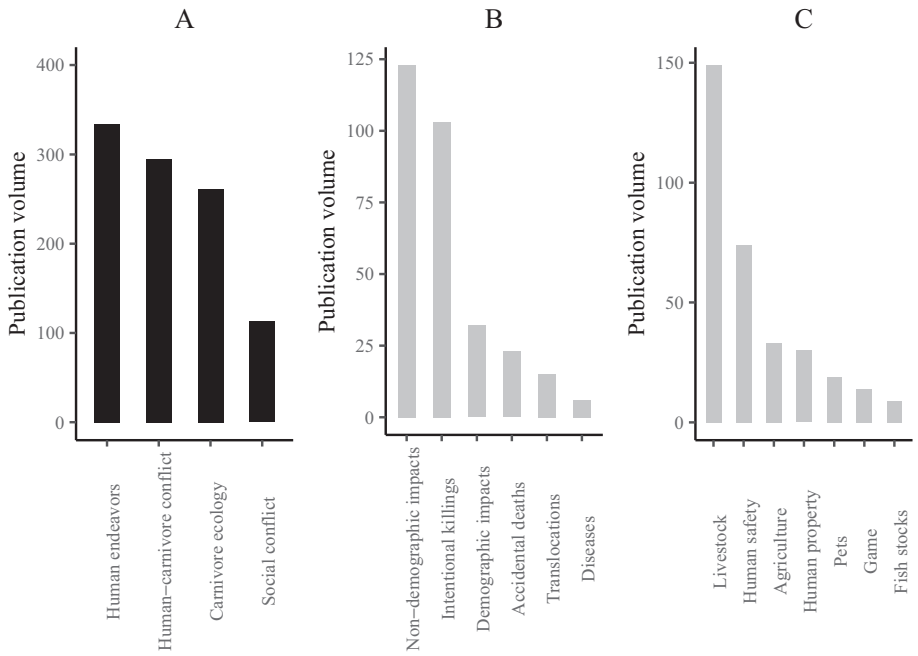

Fig. 2. Thematic focus of published research about human-carnivore coexistence. (A) Publication volume focusing on the four thematic aspects of coexistence: *human endeavors*, *human-carnivore conflict*, *carnivore ecology*, and *social conflict* over carnivores; (B) Publication volume focusing on impacts of human-carnivore conflict on carnivores. (C) Publication volume focusing on impacts of human-carnivore conflict on people.

3.3. Taxonomic focus

98.9% (n = 362) of articles referred to the interaction between *Homo sapiens* and carnivores in modern history. However, some archaeological articles (1.1%; n = 4) focused on the interaction between humans and carnivores during the Pleistocene epoch and included other *Homo* species. Two articles (0.5%) thus referred to "hominins" without specifying the species, one (0.27%) focused on *H. neanderthalensis*, and another (0.27%) on *H. antecessor*.

The distribution of coexistence research among Carnivora families significantly differed from frequencies expected by chance ($\chi^2 = 259.78$; df = 10; $p < 0.001$). Out of the 366 included articles, coexistence research studied mostly two families (Fig. 3A), Felidae (50.5%; n = 185) and Canidae (47.0%; n = 172), followed by Ursidae (20.5%; n = 75), Hyaenidae (11.5; n = 42), Mustelidae (8.2%; n = 30), and Phocidae (3.3%; n = 12). Other families (Otariidae, Herpestidae, Procyonidae, Viverridae and Mephitidae) each represented less than 1.5% (n ≤ 5) of the coexistence research. 8.5% of articles (n = 31) did not focus on any specific Carnivora family, genus or species and addressed the entire group of carnivores. 108 different species of carnivores were studied

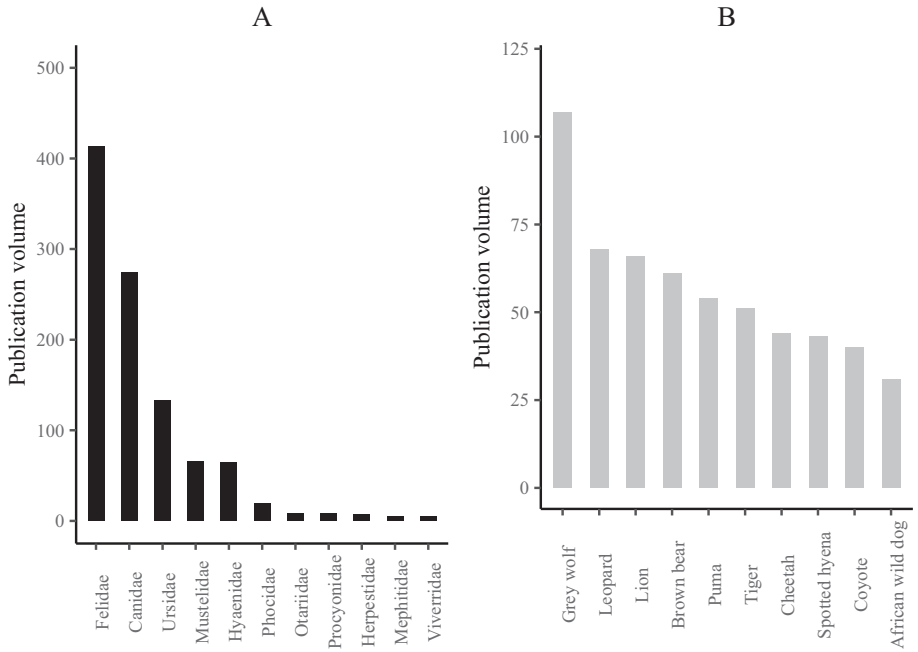

Fig. 3. Taxonomic focus of published research about human-carnivore coexistence. (A) Publication volume for all Carnivora families studied by at least one article. (B) Publication volume for the 10 most studied species of carnivores.

across all articles; gray wolves (*C. lupus*; 23.2%; n = 85), leopards (*P. pardus*; 15.3%; n = 56), lions (*P. leo*; 13.4%; n = 49) and brown bears (*Ursus arctos*; 13.1%; n = 48) were studied most frequently (Fig. 3B).

As predicted, research focus was positively related to body mass (likelihood ratio $\chi^2 = 37.25$; df = 1; $p < 0.001$) and diet (likelihood ratio $\chi^2 = 33.38$; df = 4; $p < 0.001$) of the focal carnivore species but, contrary to predictions, was not significantly related to its conservation status (likelihood ratio $\chi^2 = 2.04$; df = 4; p = 0.729) (Fig. 4). Further exploration of the effect of diet on publication volume revealed that carnivorous species were more frequently studied than herbivorous and omnivorous species (both Z ratios >3.34; $p < 0.007$) (see Appendices E1 and E2 for individual test results).

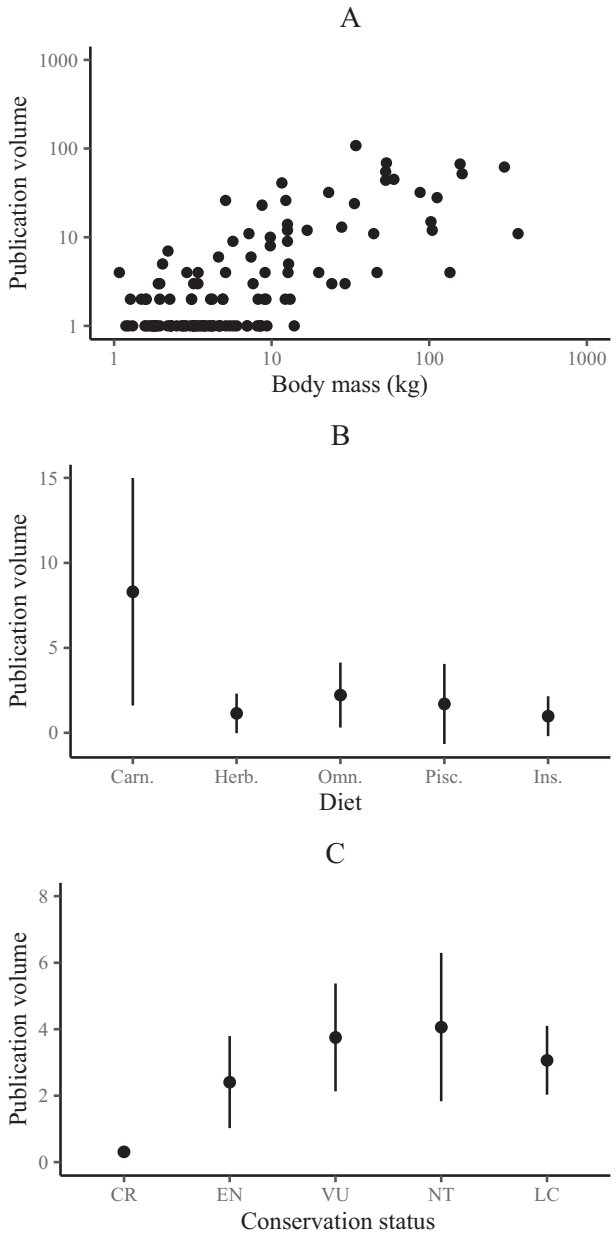

Fig. 4. Effect of ecological variables on research interest for carnivores. (A) Publication volume as a function of body mass of the focal carnivore species, plotted on a log-log scale to aid in visualization. (B) Publication volume as a function of diet of the focal carnivore species ('Carn.' = 'carnivorous'; 'Herb.' = 'herbivorous', 'Omn.' = 'omnivorous', 'Pisc.' = 'piscivore'; 'Ins' = 'insectivorous'). (C) Publication volume as a function of global conservation status of the focal carnivore species (CR = 'critically endangered'; EN = 'endangered'; VU = 'vulnerable'; NT = 'near threatened'; LC = 'least concern'). No carnivore species with 'extinct' or 'deficient data' status were studied. In (A), black dots represent the publication volume focusing on each Carnivora species. In (B) and (C), black dots show the estimated marginal means, with their standard errors.

3.4. Geographic focus

Publication volume significantly differed among continents for study areas ($\chi^2 = 34.44$; df = 5; $p < 0.001$) and residency of lead authors ($\chi^2 = 76.48$; df = 5; $p < 0.001$) (Fig. 5). Out of 366 articles, studies were conducted primarily in Europe (30.9%; n = 113), Asia (27.6%; n = 101), North America (25.4%; n = 93) and Africa (20.2%; n = 74) (Fig. 5; see Appendix F1 for a world map of coexistence research); 12.8% of articles (n = 47) did not focus on a particular study area. A majority of articles were led by authors from western countries: 39.3% (n = 144) were conducted by Europeans and 37.7% (n = 138) by North Americans (Fig. 5; see Appendix F2 for a world map of coexistence research). The lead author's residency was not available for 1.9% of articles (n = 7). Further, aside from 79 (21.6%) articles that did not study a specific system and 106 articles that studied mixed landscapes (29.0%), rural areas received significantly more attention (42.9%; n = 157) than urban areas (6.6%; n = 24) ($\chi^2 = 26.62$; df = 1; $p < 0.001$).

As predicted, publication volume was positively related to carnivore richness (likelihood ratio $\chi^2 = 166.61$; df = 1; $p < 0.001$) and economic development (likelihood ratio $\chi^2 = 91.32$; df = 3; $p < 0.001$) of the study area country, but, contrary to prediction, the positive relationship with human population was not statistically significant (likelihood ratio $\chi^2 = 2.11$; df = 1; p = 0.146) (Fig. 6). Developed countries were significantly more studied than any other level of development (all Z ratios >5.45; $p < 0.001$; see Appendices G1 and G2 for individual test results). Similarly, publication value was positively related to the economic development of the country of residency of lead authors (likelihood ratio $\chi^2 = 174.40$; df = 3; $p < 0.001$) and to carnivore richness (likelihood ratio $\chi^2 = 156.32$; df = 1; $p < 0.001$), but not to human population (likelihood ratio $\chi^2 = 0.90$; df = 1; p = 0.344) (Fig. 7). Again, developed countries were significantly more studied than any other level of development (all Z ratios >5.75; $p < 0.001$) (see Appendices H1 and H2 for individual test results).

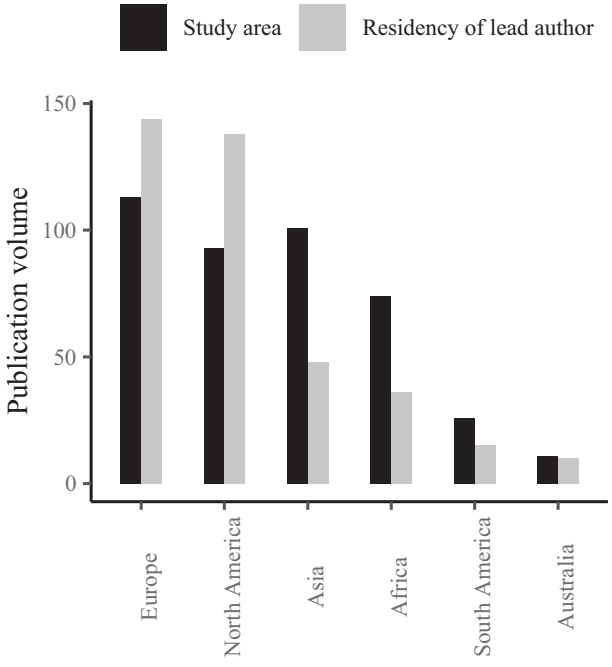

Fig. 5. Geographic focus of published research about human-carnivore coexistence by continents according to study area and residency of lead author.

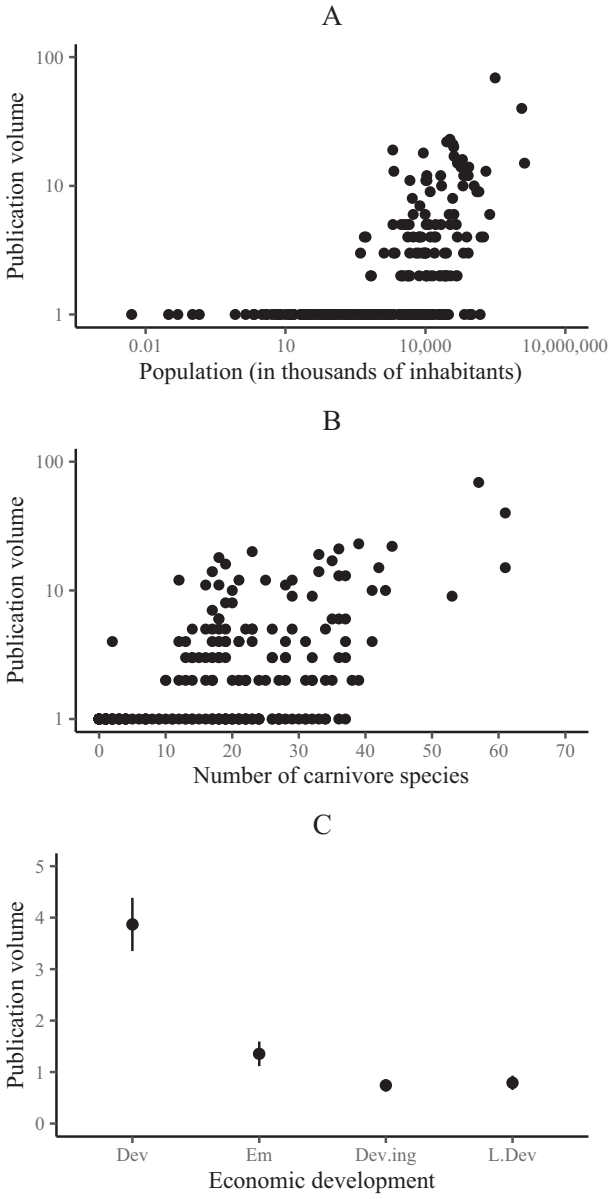

Fig. 6. Effect of three variables on coexistence research interest for countries where study occurred. (A) Publication volume as a function of human population (plotted on log-log scale to aid in visualization). (B) Publication volume as a function of carnivore species richness (publication volume plotted on a log scale to aid in visualization). (C) Publication volume as a function of economic development ('Dev' = 'developed'; 'Em' = 'emerging'; 'Dev.ing' = 'developing'; 'L.Dev' = 'least developed'). In (A) and (B), black dots represent the publication volume of each country. In (C), black dots show estimated marginal means with their standard errors.

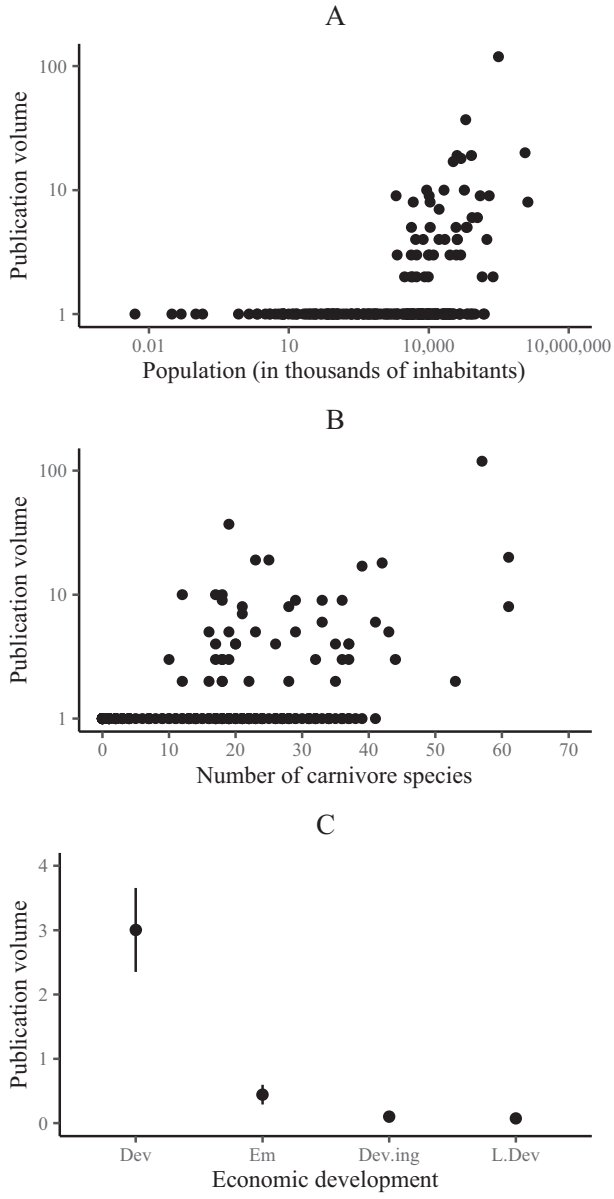

Fig. 7. Effect of three variables on coexistence research interest for countries of residency of lead authors. (A) Publication volume as a function of human population (plotted on log-log scale to aid in visualization). (B) Publication volume as a function of carnivore species richness (publication volume plotted on log scale to aid in visualization). (C) Publication volume as a function of economic development ('Dev' = 'developed'; 'Em' = 'emerging'; 'Dev.ing' = 'developing'; 'L.Dev' = 'least developed'). In (A) and (B), black dots represent the publication volume of each country. In (C), black dots show estimated marginal means with their standard errors.

4. Discussion

The idea of coexisting with carnivores is not new (Herrero, 1970) but our systematic map indicates that the term appeared explicitly in the scientific literature starting in 1987. Since then, the volume of publications focusing on human-carnivore coexistence has increased exponentially so that 57 articles used the term in 2019. Interestingly, few articles (3.8%) defined the term "coexistence" and those that did used rather inconsistent definitions. Thematically, coexistence research focused mostly on *human endeavors* (91.3%), *human-carnivore conflicts* (80.6%) and *carnivore ecology* (71.3%), with less emphasis on *social conflict* (30.9%). The literature also focused primarily on larger carnivorous species, with almost half of the articles studying two of the 18 Carnivora families, Felidae and Canidae. Research was conducted primarily in Europe, Asia, North America and Africa, by mainly European and North American authors.

4.1. Thematic focus

The recent increase of coexistence research might reflect in part increasing numbers of encounters between humans and carnivores (Exposito-Granados et al., 2019; Lozano et al., 2019). It might also be due to an effort to shift conservation terminology towards a positive framework, manifested by preferring the term "coexistence" to

"conflict" (Frank and Glikman, 2019; Nyhus, 2016; Peterson et al., 2010; Pooley et al., 2021; Redpath et al., 2013) or to integrate the study of human-carnivore interactions at the scale of landscapes (Hersperger et al., 2021). However, while the four articles that defined coexistence by citing other authors used the same definition from Carter and Linnell (2016), other definitions of coexistence seemed inconsistent.

Systematic mapping within each of the thematic aspects of coexistence provided further insight into coexistence research focus. *Human endeavors*, studied by almost all articles, included research on human attitudes towards carnivores and the economic impact of carnivores. Less than half of articles studying *carnivore ecology* did so at the population level, suggesting more research is warranted to better understand demographic responses of carnivores when evaluating human-carnivore coexistence. A few articles studied *carnivore ecology* as the only theme of focus. For example, (Vizcaychipi et al., 2016) studied zoonotic parasites in bush dogs (*Speothos venaticus*) but did not investigate transmission to humans or pets and thus did not explicitly consider conflict. However, as described by the authors, their study did inform measures to prevent disease transmission between coexisting human and animal populations, providing insight into coexistence.

Research on *human-carnivore conflict* included articles addressing impacts to both humans and carnivores, in similar proportions. Typically, human–carnivore conflict occurs when the behavior of carnivores poses a direct and recurring threat to people's safety or livelihood and, in response, persecution of the species ensues (Zimmermann et al., 2010). Impacts on human livelihoods focused mainly on livestock depredation and human safety, as predicted and consistent with prior studies (Exposito-Granados et al., 2019; Lozano et al., 2019). The two most studied impacts of conflict on carnivores were non-demographic impacts (including shifts in activity patterns, home ranges, and diets) and intentional mortality (including legal and illegal killings of carnivores). While reducing carnivore depredation and attacks on humans are generally recognized as necessary to achieve coexistence, whether legal killing of carnivores should be reduced is still debated among conservation professionals (Lute et al., 2018). Protecting humans at immediate risk, population control, or recreational hunting are examples of justifications of intentional killing accepted by some practitioners (Lute et al., 2018). The consequences of non-demographic impacts to carnivores are also ambiguous. For example, temporal avoidance of humans, such as increased nocturnal activity, might suggest behavioral plasticity that can lead to lower human-caused mortality (Carter et al., 2012; Oriol-Cotterill et al., 2015), but it might also alter carnivore hunting success, individual fitness, and population demographics (Lamb et al., 2020; Oriol-Cotterill et al., 2015). These results highlight the need for a better consensus around the specific goals of coexistence research and practice.

As predicted, research focused on *social conflict* was less common than studies on *human endeavors*, *carnivore ecology*, and *human-carnivore conflict*. Yet, some authors have suggested that the human-human dimensions of conservation conflicts are fundamental (Redpath et al., 2013) and have stressed the need to address the social aspect of human-carnivore relations (Carter et al., 2019; Dietsch et al., 2019; Madden and McQuinn, 2014; Treves and Karanth, 2003). Indeed, conservation approaches have focused on mitigating human-carnivore conflicts by non-lethal management and by economic compensation programs, but less on understanding the underlying causes of social conflict (Madden and McQuinn, 2014).

Although Carter and Linnell (2016) provide a useful framework for coexistence, including mechanisms such as governance and co-adaptation creates a long and complex definition. We suggest a more succinct definition of coexistence would be useful in both research and practice. In an effort to enhance understanding of coexistence and to focus future research, we offer a simplified, formal definition of coexistence stemming from our systematic map and existing definitions (Carter and Linnell, 2016; Chapron and Lopez-Bao, 2016; Glikman et al., 2021; Hill, 2021; Hull et al., 2016; Morehouse and Boyce, 2017). Our definition explicitly incorporates the 4 thematic aspects of coexistence we encountered in the literature: *Co-occurrence of sustainable carnivore populations and human endeavors with minimal human-carnivore and human-human conflict* (see Fig. 8). A sustainable carnivore population has sufficient numbers and geographic distribution such that it can persist over the long-term (Soulé, 1987), including abundant and widespread carnivores or formerly endangered carnivores that have been successfully recovered.

4.2. Taxonomic focus

The literature focused mostly on the Carnivora families Felidae and Canidae and, to a lesser extent, on Ursidae, Hyaenidae and Mustelidae. As predicted, publication volume was positively related to body mass and degree of carnivory of focal carnivore species. These results could be the consequence of several possible drivers motivating coexistence research. First, large and carnivorous species might be considered more dangerous. Carnivory, rather than omnivory or herbivory, is more likely to bring carnivores into competition with humans for prey such as livestock, pets, or game, and might represent a direct predation threat to people themselves (Brooke et al., 2014). While humans might encounter smaller carnivores more frequently, large body mass is likely to increase the intensity of damage caused to humans and their property (Brooke et al., 2014; Nyhus, 2016). Such important damage is more likely to affect human livelihoods and to raise stronger reactions (Nyhus, 2016). Additionally, size and potential dangerousness to humans have been related to human perception of charisma (Albert et al., 2018; Johnson et al., 2010; Martin-Lopez et al., 2008), and conservation literature tends to be biased towards charismatic species such as large carnivores (Ducarme et al., 2013). In fact, the four most studied species in coexistence research (gray wolves, leopards, lions, and brown bears) were all listed among the 20 most charismatic species, based on public surveys and depictions of carnivores in media (Albert et al., 2018; Arbieu et al., 2019). Whether the taxonomic focus of coexistence research is related to the intensity of impacts on human livelihoods or to a perception bias remains unclear. More research on smaller carnivores, which can also come into conflict with humans (Akpona et al., 2015; Herr et al., 2009), would further inform mechanisms underlying tolerance and coexistence.

Contrary to predictions, research focus was not related to conservation status of carnivore species. This might be because conservation actions for threatened carnivores rely only partially on the coexistence strategy and also include the separation model. For example, protected areas where human activity is limited also play an important role in carnivore conservation (Packer et al., 2013). Coexistence might be considered a better strategy for recovering less vulnerable carnivores (Chapron et al., 2014) because it implies a lower level of protection and a higher risk for conflict and carnivore mortality (Lamb et al., 2020; Packer et al., 2013). More generally, conservation literature does not necessarily focus on the most endangered species (Brooke et al., 2014). Research might also be motivated by local conservation status of a given species, more so than by its global conservation status. For example, wolves (*C. lupus*), while globally classified as 'least concern' species (IUCN Red list, 2020), are protected by the Endangered Species Act in some regions of the United States (ECOS, 2020). More studies focused on threatened and endangered carnivores might increase the conservation impact of coexistence research.

4.3. Geographic focus

As predicted, study areas were located primarily in Europe, Asia, North America and Africa, and in countries with higher carnivore richness and economic development. Contrary to predictions, publication volume was not significantly related to countries' human population in our statistical models. We suspect that this was likely due to a stronger effect of economic development in our models and also note that the

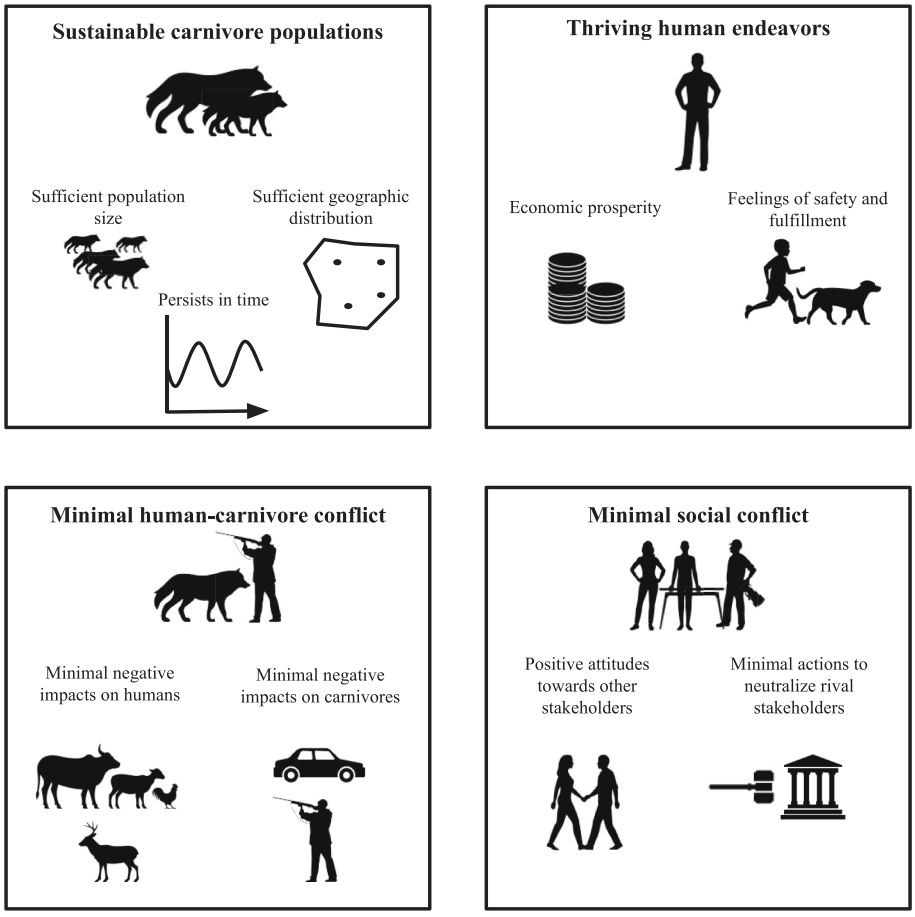

Fig. 8. Four pillars of human-carnivore coexistence. Each pillar lists criteria that can be measured with social and ecological approaches.

relationship with human population was positive, as expected. Certainly, considerable overlap of carnivores and people in highly populous countries such as India elevates the potential for human-carnivore conflict (Boomgaard, 2010). Human-carnivore conflict, such as attacks on people or livestock, is more frequent and has a larger impact on human livelihoods in developing countries, because populations are more rural and thus more in contact with carnivores (Inskip and Zimmermann, 2009; Treves et al., 2004) and more dependent on agricultural revenues (Lozano et al., 2019; Ward, 1987). Therefore, the higher publication volume of research conducted in developed countries likely reflects better access to funding for scientific research rather than the degree of impact on humans. In addition, our search was designed in English, and only articles in English language were included, similarly to other systematic reviews (Amano et al., 2016; Knox et al., 2021). English proficiency is generally positively correlated to economic development (EF English Proficiency Index, 2019). Thus, the overrepresentation of developed countries in this study might reflect different access to publication (financially and linguistically).

Our findings also reflected that lead authors originated primarily from Europe and North America. This might be a result of limiting the search to the sole language of English and to the Web of Science database, as it might not allow us to capture analogous concepts expressed by different words or phrases in other languages (e.g., see Pooley et al. (2021) for examples of coexistence-related concepts in Zulu). Further, important cultural differences exist in the way people perceive their relation to wildlife, including to carnivores. The North American ideal of wilderness, also popular in Europe, conveys a duality between humans and the rest of nature (Chapron et al., 2014; Linnell et al., 2015) that could appear nonsensical to someone believing that all forms of life share landscapes and moral universes (Pooley, 2021). For example, Clark and Slocombe (2009) described human-bear relations for aboriginal 'First Nation' people in Canada as revolving around the ideas of respect and kinship, showing examples of aspects that western authors might not fully grasp. Similarly, in a survey conducted in South India, Thekaekara et al. (2021) reported that respondents conceptualizing elephants as "other-than-human persons" were the most inclined to coexist with them. Thus, understanding of coexistence would likely benefit from the contribution of authors from more diverse cultures, able to translate and convey notions from other languages and worldviews to the international scientific community.

4.4. Conclusion

In summary, our findings highlight several future priorities for human-carnivore coexistence research. We suggest a concise definition of "coexistence", developed from the existing body of human-carnivore coexistence literature and centered around four measurable thematic aspects (*sustainable carnivore populations, sustainable human endeavors, minimal human-carnivore and social conflict*), can help compare research results across articles, draw better conclusions on the outcomes of conflict mitigation or other conservation actions, and advance understanding of the mechanisms fostering human-carnivore coexistence. In particular, our study demonstrated that social conflict is the least studied aspect of human-carnivore coexistence, even though it is a major driver of conflict regarding carnivores. Conservation professionals have identified fear of carnivores and mistrust between decision-makers and local communities as leading causes of conflict between humans and carnivores (Lute et al., 2018). For example, conflict between leopards (*Panthera pardus*) and local stakeholders in Northern India stemmed from the stakeholder's conflictual relationship with governmental

authorities, despite positive attitudes towards leopards themselves (Dhee et al., 2019). Moreover, public behaviors can directly influence carnivore management and interactions, for example by voting to implement policies of reintroduction (Niemiec et al., 2020) or by bear-proofing garbage containers (Lischka et al., 2018). Thus, understanding human attitudes towards carnivores and the underlying causes of social conflict would help build more effective carnivore conservation plans that go beyond technical or economic approaches such as non-lethal carnivore management or compensation payments (Madden and McQuinn, 2014). This should become easier as more tools become available to evaluate emotions among stakeholder groups (Arbieu et al., 2021). Further, coexistence should be understood as a dynamic process, shaped by ongoing negotiations between stakeholders (Konig et al., 2020; Kshettry et al., 2020). A stronger emphasis on the social science underlying coexistence would also advance understanding of social tolerance of carnivores, a critical requirement for coexistence (Carter and Linnell, 2016). Finally, human-carnivore coexistence has been primarily studied under the prism of western culture. Broadening the approach could be done by incorporating local (Lozano et al., 2019) and multicultural knowledge (Schroer, 2021) into the conception of coexistence research projects and conservation strategies.

Statement of ethics

None to declare.

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CRediT authorship contribution statement

Cassandre Venumière-Lefebvre: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Software; Visualization; Writing - original draft. **Stewart Breck**: Conceptualization; Funding acquisition; Methodology; Supervision; Writing - review & editing. **Kevin Crooks**: Conceptualization; Data curation; Investigation; Methodology; Supervision; Validation; Writing - review & editing.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109515.

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