Human-carnivore relations: A systematic review

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A B S T R A C T

We conducted a systematic review of 502 articles, published between 2000 and 2016, to characterize the research on human-carnivore relations according to (i) temporal and geographical distribution, (ii) biology, (iii) relations between carnivores and humans, (iv) social actors, (v) drivers of change, (vi) management, and (vii) applied methods. We performed a detrended correspondence analysis and Kruskal-Wallis tests to identify and describe thematic clusters used in human-carnivore relations research. Our results show that research is deeply biased so far, and four important knowledge gaps were detected. First, we found more studies had been conducted in the Global North than in the Global South, although risks and benefits of living alongside carnivores exist in the Global South equally. Second, most research focused on large predators, while small and mediumsized carnivores are also source of damages and ecosystem services. Third, relations were often framed around conflicts, with little attention to possible ecosystem services. Fourth, most research was carried out using natural sciences methods, despite methods from the social sciences having much to offer in this context. Research fell into seven thematic clusters focusing on: (1) North-American bears, (2) African large carnivores, (3) social research in America, (4) meso-carnivores, (5) Asian felids, (6) conflicts with the grey wolf, and (7) damages to human property. These results highlight the need for more integrative, social-ecological research on humancarnivore relations. We discuss how addressing existing knowledge gaps could contribute to mitigating conflicts as well as fostering coexistence between humans and carnivore species.

1. Introduction

It is becoming increasingly clear that effective conservation requires interdisciplinary approaches that connect the natural and social sciences (Pooley et al., 2014; Tallis and Lubchenco, 2014; Martín-López

and Montes, 2015). This challenge is particularly evident for carnivore conservation, which involves a series of deep and interrelated ecological and social relations (Carter et al., 2014; Darimont et al., 2018; Dressel et al., 2018; Lischka et al., 2018), including the fact that carnivores can threaten lives and livelihoods in rural areas, while their

tangibly influence the state of nature and people's quality of life, and include land-use change, climate change, species introductions and poaching (MA, 2005; Rounsevell et al., 2010). For instance, climate change in the Himalaya region has led to increasing rates of livestock depredation by the snow leopard (Uncia uncia) (Aryal et al., 2014).

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importance as keystone species is recognized mainly by urban societies (Kruuk, 2002; Inskip and Zimmermann, 2009; Ripple et al., 2014).

Although no study has systematically addressed the role of socialecological approaches to understand human-carnivore relations, recent studies suggest that a social-ecological perspective is rapidly gaining traction (Pooley et al., 2016; Dressel et al., 2018; Lischka et al., 2018). The application of a social-ecological approach to study human-carnivore relations requires consideration of many ecological and social components as well as their relations, including: communities of carnivore species and their ecosystems, the different actors' perceptions and values regarding specific carnivores species, and the drivers (both indirect and direct) that lead to changes in the way humans and carnivores relate, including through changes in governance structures that guide carnivore management (Lischka et al., 2018).

Both perceptions and values have been defined differently by scholars studying human-animal relationships (Echeverri et al., 2018). Following Bennett (2016), we refer to perceptions as the ways an individual observes, understands, interprets, and evaluates a particular carnivore species, an experience with carnivores, and a policy, management action or outcome with regard to carnivores. For values, we follow the definition given by the Intergovernmental Platform of Biodiversity and Ecosystem Services (IPBES) (Díaz et al., 2015; Pascual et al., 2017). We thus define value as the importance of a particular asset and a preference that someone has for a particular condition of a system. Therefore, in the context of human-carnivore relations, values refer to the importance given by people to carnivore species and to people's preferences for a specific condition of the system in which human-carnivore relations are embedded.

Direct and indirect drivers of global environmental change play important roles in shaping human-carnivore relations. Direct drivers

Indirect drivers refer to the underlying causes of changes in humancarnivore relations, such as changes in institutions and governance structures, economy, demography, culture or lifestyles (MA, 2005). For instance, in 2017 the US government restored endangered-species protections to the grizzly bear (Ursus arctos horribilis) in Yellowstone National Park, which may influence people's perceptions of this species as well as how people value it (Lischka et al., 2018).

In this research, we systematically reviewed the research on humancarnivore relations between 2000 and 2016 with the goals to identify key knowledge gaps and future research priorities, as well as to appraise the level of application of interdisciplinary social-ecological approaches. We adopt the term of 'human-carnivore relations' as an umbrella concept to refer to both positive and negative relationships between people and carnivores species, embracing a wide range of notions, such human-carnivore interactions (e.g. Young et al., 2015; McKay et al., 2018) or human-carnivore conflicts (e.g. Inskip and Zimmermann, 2009; Peterson et al., 2010). We further understand the term 'human-carnivore relations' to encompass both direct human experiences with carnivores, such as encounters (e.g. Wine et al., 2015; Kauhala et al., 2016), and indirect relationships expressed via people's attitudes (e.g. Kansky et al., 2014; Dressel et al., 2015), perceptions (e.g. Kellert, 1985; Morales-Reyes et al., 2017), values (e.g. Herrmann et al., 2013; Dietsch et al., 2016) and behaviours (e.g. Mattson and Ruther, 2012; Browne-Nuñez et al., 2015) towards carnivores.

Our specific aims were to (1) characterize current scientific literature on human-carnivore relations according to (i) temporal and geographical distribution, (ii) biological components (i.e. taxonomy, biomes), (iii) relations between carnivores and humans in terms of carnivores' detrimental and beneficial contributions to human wellbeing (i.e., conflicts and ecosystem services), human-nature

connections, human perceptions, attitudes and values related to carnivores, (iv) type of social actors or stakeholders involved, (v) drivers of change considered, and (vi) management strategies; (2) identify which methodological approaches and tools have been applied; and finally (3) characterize different foci in human-carnivore relations research through the identification of internally coherent thematic clusters.

2. Methods

We conducted a systematic review of English language scientific articles dealing with conflicts and/or ecosystem services that carnivores provide to society. To perform this systematic review, we followed the guidelines of Pullin and Stewart (2006). Systematic reviews aim to summarize and appraise results from a large body of research (Pullin and Knight, 2009). In doing so, this method follows a strict protocol of searching and inclusion criteria of published information to guarantee transparency and minimize the sources of bias. The first and last authors of this study searched the Scopus database by using a search string that combined different terms related to human-carnivore relations, including 'conflict*', 'ecosystem service*', 'human-carnivore relation*', and to the taxonomic group of 'carnivores' (see Appendix A for the full search string). The emphasis on conflicts and ecosystem services was because these aspects are at the core of social-ecological approaches (Ostrom, 2009; Binder et al., 2013; Guerrero et al., 2018) – that is, conflicts can arise from social-ecological relations when socially valued activities interfered with carnivore conservation (e.g. livestock damage), while services may be provided if carnivores support socially valued activities (e.g. in the case of carnivore-related tourism). The search was applied to title, abstract and keywords from 2000 to 2016, and returned an initial total of 1411 articles. We then restricted the search to peer reviewed articles published in international journals (i.e., we excluded book chapters and conference papers) in English, and this yielded 1358 articles.

The final number of studies reviewed in detail was refined on the basis of a two-step process (e.g., Nieto-Romero et al., 2014; Dressel et al., 2015; Hevia et al., 2017; see Appendix B): (1) title and abstracts, and (2) full content of the article. We first screened titles and abstracts to ensure we only included empirical studies (i.e., we excluded reviews and conceptual papers). Further, we only included articles dealing with relations between humans and terrestrial/freshwater carnivores. We excluded articles focused strictly on the biology and ecology of carnivores because these do not deal with human-carnivore relations, and articles investigating marine carnivores (e.g. sea lions and seals) because conflicts in those cases largely relate to marine aquaculture and fishing (e.g. Würsig and Gailey, 2002; Pont et al., 2016). Then, we reviewed selected articles in full, using the same aforementioned inclusion criteria. In the second step, we further excluded articles mentioning only superficially in the introduction and discussion the terms 'conflict' or 'ecosystem service', for example to motivate the

work or suggest future research needs. This procedure provided a final set of 502 articles[2] for in-depth review.

Because findings of systematic reviews strongly depend on decisions about how information from the selected studies is coded for further analysis (Higgins and Green, 2011), the first two authors undertook the same process for coding the information on a random sub-sample of papers. Once consistency in the coding of information had been achieved among them, they provided explicit, written guidelines and practical procedures to all researchers who collaborated in the creation of the database.

Besides the general characteristics of the articles (i.e. year of publication, country where the research was conducted), we coded them

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according to various relevant components of social-ecological systems mentioned in each one: (1) biological components, such as biome type (based on MA, 2005), and carnivore family and species; (2) detrimental and beneficial contributions of carnivores to humans wellbeing, i.e. whether the article mentioned conflicts or ecosystem services provided by carnivores, type of conflict (based on Kruuk, 2002; Peterson et al., 2010), and type of ecosystem service (based on the categories of beneficial nature's contributions to people of Díaz et al., 2018); (3) whether the research mentioned any type of human-nature connections, according to Ives et al. (2017); (4) whether human perceptions, attitudes and values were analyzed (based on Jacobs et al., 2018); (5) type of direct and indirect drivers of change according to the Millennium Ecosystem Assessment (MA) (2005); (6) type of social actor involved; and (7) type of management strategy mentioned by authors (modified from Inskip and Zimmermann, 2009). A detailed description of these variables can be found in Appendix C. Furthermore, we coded methodological aspects regarding type of data collected, type of data analysis, whether local ecological knowledge was used as a source of information, and whether planning of scenarios was conducted to envision futures of human-carnivores relations and their management. For all these variables, we used the relative frequency of different types of studies to illustrate the current state of knowledge and research interest on the different components of social-ecological systems. G-tests (Sokal and Rohlf, 1981; McDonald, 2009) were performed to compare relative frequencies of the considered variables to check for geographical differences in the research of human-carnivore relations.

In addition, to identify clusters on human-carnivore relations research we performed a detrended correspondence analysis (DCA) (Hill and Gauch, 1980) using the words that hold meaning for this

research extracted from the content of articles. We therefore excluded meaningless words, such as articles or prepositions. We initially built a matrix containing all abundant meaningful words occurring in the individual papers. Using Ward's method we conducted a cluster analysis of the complete dataset of words to divide the papers into groups where within each group, there was a significantly higher co-occurrence of words based on a permutation test as when comparing co-occurrences between groups. In a next step, these groups were visualized and further analyzed within a DCA. We opted for the DCA since it better deals with long gradients and high turnover rates in terms of co-occurrences of words than other ordination approaches. In the two-dimensional space depicted by the DCA, words that are close to each other co-occur together in papers, while words that are distant from each other were present in different papers (for more details see for example Dufrene and Legendre, 1997; Paterlow et al., 2017). This analysis was conducted using R (R Core Team, 2016) with the next libraries: 'tm' for text mining, 'plyr' for data sorting, 'vegan' for the DCA analysis, 'cluster' for cluster analyses, and 'labdsv' to estimate the importance of the words for each cluster. We performed Kruskal-Wallis tests and a posteriori multiple comparisons to determine differences in quantitative variables (i.e., number of conflicts, ecosystem services, drivers, social actors and management actions) among the obtained clusters. We conducted Gtests and Kruskal-Wallis tests with the software Statistica 10 (StatSoft Inc, 2011).

3. Results

3.1. Temporal and geographical distribution

Since 2000 the number of published studies rapidly increased, with a peak in 2015 (Fig. 1a). The largest proportion of research was performed in North America, northern and Mediterranean Europe, China, India, Australia and southern Africa (Fig. 1b). By contrast, Central Europe, Central America, the Middle East, most Africa and the Asian Southeast received relatively less attention (Fig. 1b).

3.2. Biological components

Out of 12 families of carnivores, most research focused on four families: Felidae (cats; 40.4% of articles), Canidae (wolves and foxes; 38.8%), Ursidae (bears; 31.7%) and Hyaenidae (hyenas; 7.8%). This coverage does not correspond with what might be expected according to their respective number of species, that is, the families Ailuridae, Eupleridae, Herpestidae, Mephitidae, Mustelidae, Nandiniidae, Procyonidae and Viverridae were underrepresented (Fig. 1c). Most studies dealt with one species (72.9% of articles), with the grey wolf (Canis lupus; 36.7% of articles), brown bear (Ursus arctos; 33.1%), leopard (Panthera pardus; 23.9%), American black bear (U. americanus; 18.3%) and lion (P. leo; 17.9%) studied most frequently. Furthermore, 19 articles out of 502 (3.9%) dealt with reintroduced large carnivores (mainly wolves, bears and big cats), and only 13

articles (2.6%) were devoted to alien species, such as the American mink (Neovison vison), red fox (Vulpes vulpes) or raccoon (Procyon lotor). Regarding the type of biome, in absolute terms most studies were performed in mountain areas, temperate forests and agricultural systems, whereas Mediterranean ecosystems, polar environments and islands were poorly represented (Fig. 1d).

3.3. Beneficial and detrimental contributions of carnivores to society

Geography influenced the distribution of studies with respect to ecosystem services and conflicts (G = 17.37, df = 10, p = 0.067). Most articles were conducted in North America and Europe, while Australia and Latin America were underrepresented (Appendix D). Most research focused only on conflicts (61.0% of articles), followed by articles mentioning both conflicts and ecosystem services (33.7%). Only 5.4% of articles dealt with ecosystem services exclusively (Fig. 2a). Among the articles focusing on ecosystem services (Fig. 2b), 54.5% of articles referred to non-material contributions, such as recreational hunting and eco-tourism opportunities, 31.3% referred to regulating contributions, such as seed dispersal, biological control and carcass removal, and 14.2% of articles referred to material contributions, such as the provision of materials (e.g. fur) and food. We found significant differences among geographical regions regarding the study of ecosystem services. While research on non-material contributions was mainly carried out in North America (G = 16.77, df = 5, p < 0.05), research on material contributions was mainly conducted in Asia (G = 33.97, df = 5, p < 0.01) (Appendix D). We did not find geographical differences in the case of regulating contributions (G = 7.03, df = 5, p > 0.05).

Regarding conflicts (see Fig. 2c), 54.9% of articles described conflicts related to damage to human food (mainly attacks to livestock and poultry), followed by damage to human safety (21.9% of articles) and damage to human property (11.5%). Threats to biodiversity and conflicts related to stakeholder disagreements (i.e., human-human conflicts) were mentioned only by 3.6% and 8.1% of articles, respectively. Geography influenced the type of conflict considered (Appendix D). Conflicts related to human food were mentioned especially in Europe, Asia and Africa (G = 48.77, df = 5, p < 0.01), those related to human safety in North America and Asia (G = 42.5, df = 5, p < 0.01), and those concerning damages to human property in North America (G = 52.39, df = 5, p < 0.01). Finally, threats to biodiversity were mentioned more often in North America, Europe and Australia than in other regions (G = 14.06, df = 5, p < 0.05). We did not find geographical differences for human-human conflicts (G = 4.39, df = 5, p > 0.05).

3.4. Human-nature connections, perceptions and values

Only 21.9% of articles provided information of human-nature connections, of which 45.5% of articles referred to emotional connection, 35.5% to experiential connections and 19.1% to

cognitive connections (Fig. 2d). Furthermore, 29.3% of articles analyzed social attitudes and
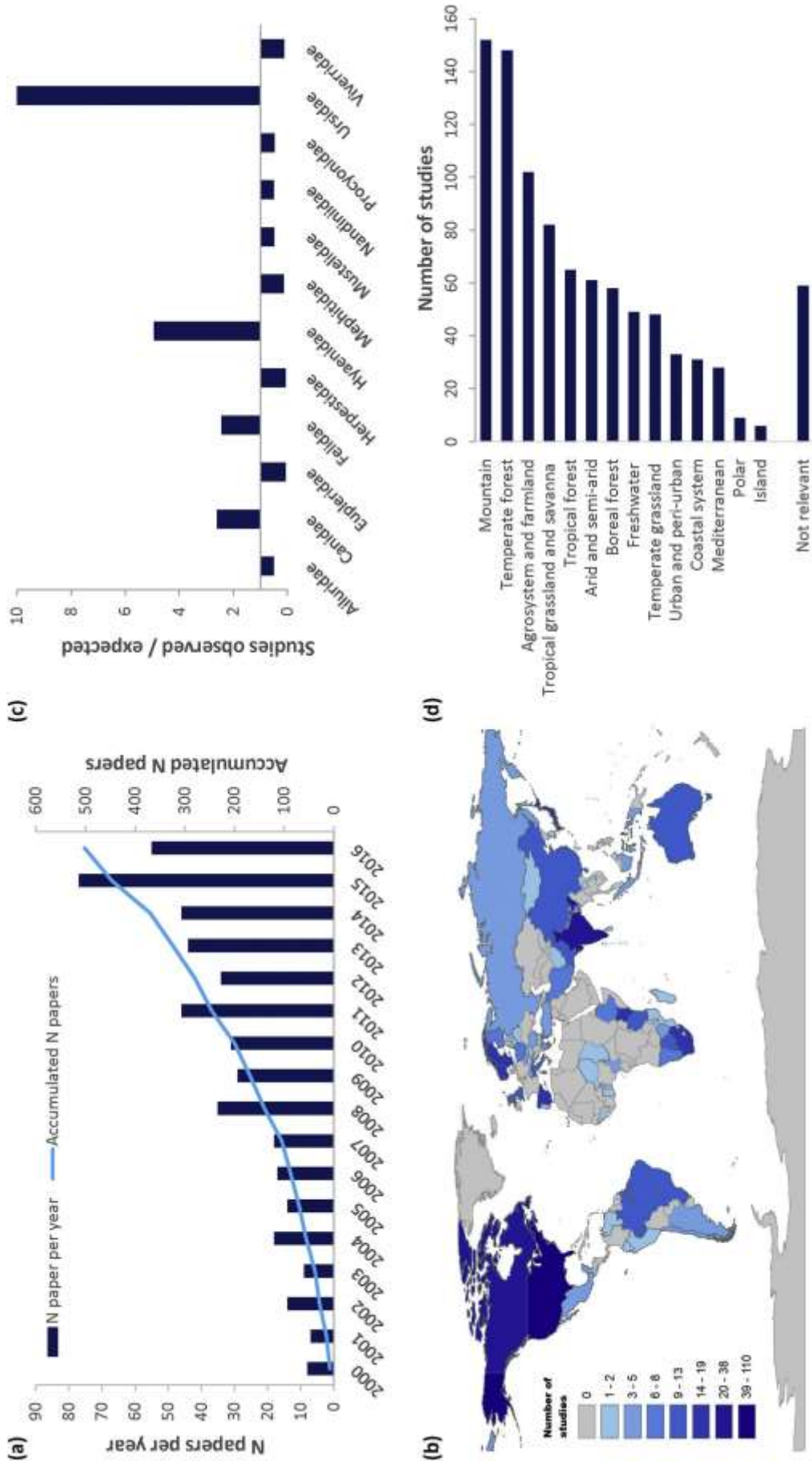
Fig. 1. Distribution of reviewed studies according to (a) time, (b) geography, (c) taxonomy, and (d) biome type. The ratio of studies observed/expected in (c) represents the number of articles found in the review for each taxonomic group (i.e. studies observed) divided by the number of expected articles given a proportional distribution based on the number of species belonging to each taxonomic group (i.e. studies expected). The articles classified as not relevant in (d) refer to those studies that do not focus on a particular biome since the scale of analysis is broader than a speci fi c site as for example articles researching for human–carnivore relations at the country level or continental scale.
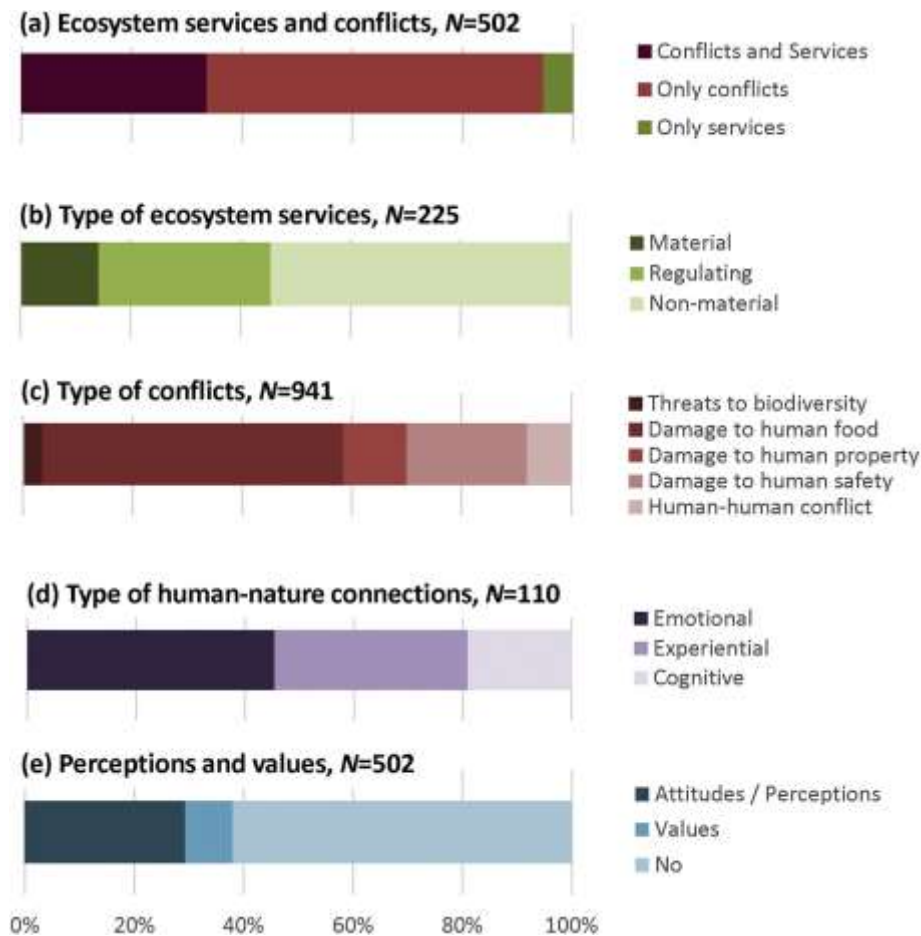
Fig. 2. Descriptive analysis of reviewed articles according to their content in terms of (a-c) ecosystem services and conflicts, (d) human-nature connections and (e) perceptions, attitudes and values.

perceptions towards carnivores, and only 8.8% mentioned any type of value related to carnivores (Fig. 2e). Existence value was the most elicited (47.7% of articles that uncovered values), followed by instrumental (38.6%), intrinsic (36.3%), relational (27.3%) and option and bequest values (11.3%).

Regarding geographical differences, we found that articles mentioning values were more frequent in North America and Europe (G = 10.92, df = 5, p = 0.053; Appendix D). However, we did not find differences related to the number of articles mentioning perceptions among regions (G = 5.47, df = 5, p > 0.05; Appendix D).

3.5. Drivers of change

More than half of the articles (56.9%) considered at least one driver of change underpinning human-carnivore relations, either direct (44.2% of articles) or indirect (55.8%), and 34.9% of articles indicated two or more drivers of change. The most frequent direct drivers mentioned were land-use change (37.9%) and overexploitation (29.8%), particularly poaching or illegal hunting (Fig. 3a), while the most frequent indirect drivers mentioned (see Fig. 3b) were changes

in conservation policies (46.7%), culture (24.2%) and increase of urban population (22.5%).

Regarding geographical differences, we found that direct anthropogenic drivers were frequently more mentioned in studies carried out in Asia and North America than in other regions (G = 16.35, df = 5, p < 0.05), while indirect drivers were more often mentioned in North America and Europe than in other regions (G = 10.37, df = 5, p = 0.065) (Appendix E). By contrast, we did not find geographical differences in the case of direct natural drivers (G = 8.96, df = 5, p > 0.05) (Appendix E).

3.6. Social actors

Most articles (90.8%) considered social actors as agents involved or to be engaged in the study of human-carnivore relations. The most frequent actors mentioned were local actors, particularly rural residents (47.2% of articles), farmers – either commercial (42.8%) or subsistence farmers (28.5%) – and hunters (26.5%) (Fig. 3c). In addition, different types of environmental managers, such as wildlife managers, protected area managers or land planning managers, were considered in 44.5% of articles (Fig. 3c).

Direct anthropogenic drivers were more frequently mentioned in Asian and North America studies (G = 16.35, df = 5, p < 0.05), while

indirect drivers were more frequently mentioned in North America and Europe (G = 10.37, df = 5, p = 0.065) (Appendix E). We did not find geographical differences related to direct natural drivers (G = 8.96, df = 5, p > 0.05) (Appendix E).

3.7. Management actions

Management recommendations to resolve or mitigate human-carnivore conflicts were mentioned in 86.2% of the articles and included non-lethal measures, community development programs and lethal control (Fig. 3d). Overall, non-lethal measures were the most widely considered, particularly those aiming to alleviate conflicts between large carnivores and livestock. Thus, 29.3% of articles considered the use of deterrents and barriers (e.g., specialized electric fencing, lights and loud noises), 25.2% of articles mentioned different livestock
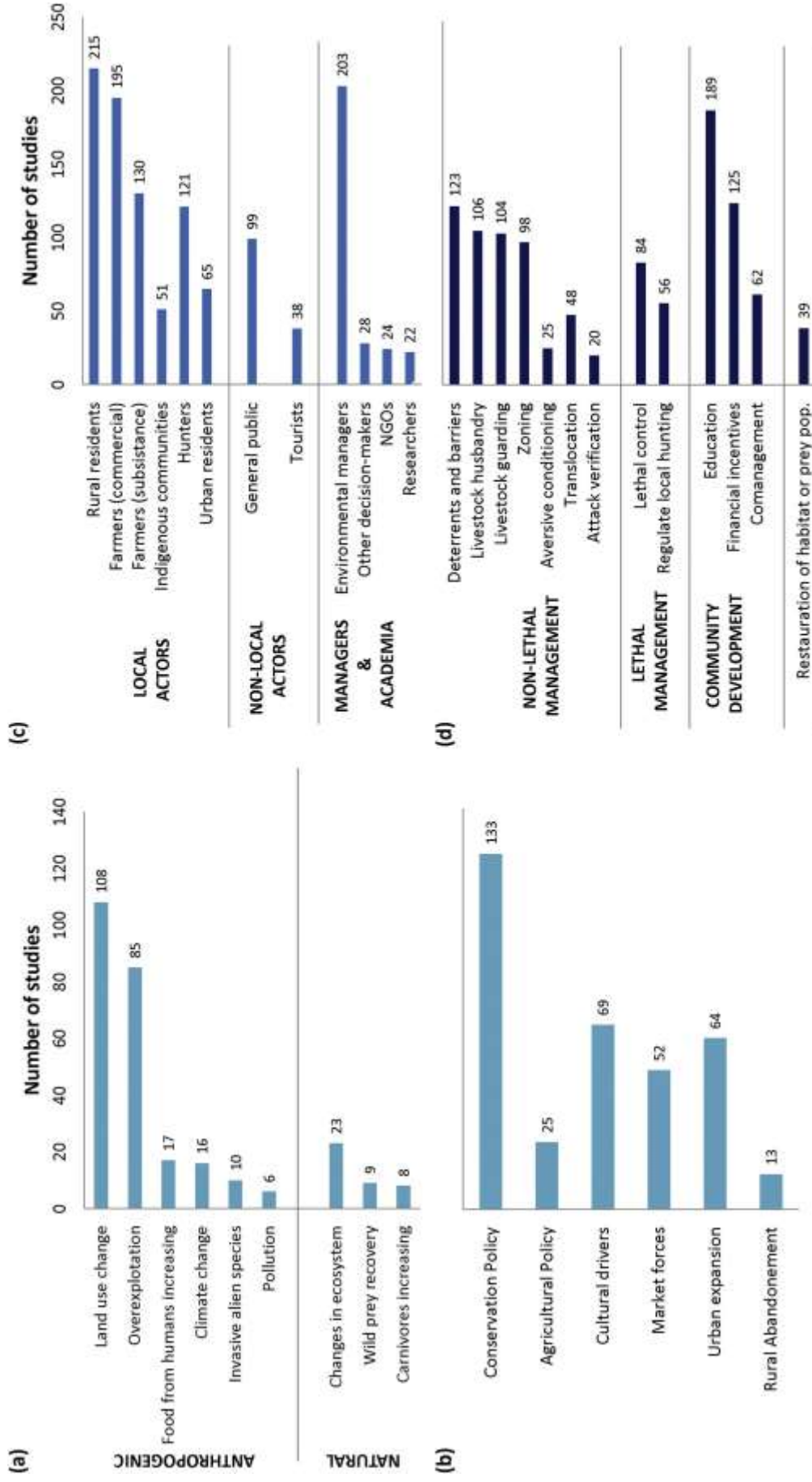
Fig. 3. Number of reviewed studies that considered (a) direct drivers of change both anthropogenic and natural, (b) indirect drivers of change, (c) types of social actors, and (d) management strategies for dealing with human-carnivore conflicts.

husbandry techniques, 24.7% of articles suggested the use of animals for livestock guarding (mainly dogs), and 23.3% of articles considered zoning as a management action, i.e. separating livestock grazing from carnivores' habitat. Other actions such as translocations, aversive conditioning and verification of attacks were less frequently mentioned (< 12%).

Management tools that target community development were frequently mentioned, in particular education programs (45.0% of articles) and financial incentives (29.8%). Financial incentives included compensation for damages, payments for ecosystem services and development of carnivore-based tourism. In relation to lethal control, the selected removal of individuals and regulation of permissions for hunting carnivores were suggested in 33.3% of articles. Nevertheless, only 22.1% of articles mentioning management measures actually evaluated an intervention.

Regarding geographical differences, we found that non-lethal measures were more frequently mentioned in articles with case studies in Asia, North America and Africa than in other regions (G = 27.06, df = 5, p < 0.01; Appendix E). We also found that articles conducted in Asia and North America mentioned community-based management mechanisms more often than those conducted in other regions (G = 27.52, df = 5, p < 0.01), and studies in North America mentioned lethal control more often than in other regions, particularly Africa and Latin America (G = 12.17, df = 5, p < 0.05; Appendix E).

3.8. Methodological approaches used

Empirical research on human-carnivores relations typically applied quantitative methods (84.9% of articles) and was based on quantitative data only (80.1%). A small percentage of articles used qualitative (12.5%) or mixed datasets (7.4%) (Fig. 4a), and only 4.8% of articles analyzed results through qualitative analyses (Fig. 4b). We found that data collection methods differed among geographical regions (Appendix F). Studies in North America and Europe used more quantitative and qualitative data collection methods, while methods to collect mixed-data were more prevalent in Asia than other regions (G = 23.32, df = 10, p < 0.05). Methods for data analyses also differed among regions (Appendix F). Quantitative methods were more often applied in studies conducted in North America and Europe, while descriptive methods were more often applied in studies conducted in Asia than in other regions (G = 25.74, df = 10, p < 0.05).

Of all methods used to collect data, biological sampling (25.2% of articles) and structured questionnaires (24.1%) were the most used (Fig. 4c). Documents analysis (15.1%) and interviews (13.5%) were also relevant, while other methods, such as participant observation or focus groups, were applied in < 10% of articles. Only 8.4% of the articles used local ecological knowledge as a source of information (Fig. 4d). Studies conducted in Asia used local ecological knowledge more often than studies conducted in other regions (G = 14.54, df = 5, p < 0.05; Appendix F). Finally, only 5.6% of the articles developed scenarios to envision futures regarding human-carnivore relations

(Fig. 4e). Future scenarios were applied in North America more often than in other regions (G = 15.02, df = 5, p < 0.05; Appendix F).

3.9. Clusters of human-carnivore relations research

We identified seven distinct clusters of research based on the DCA (Fig. 5). These clusters were distributed along two main axes. The first axis (X-axis) represented a gradient between those studies conducted in the Global North (positive scores) versus the Global South (negative scores) (Fig. 5). Mostly towards positive scores of the X-axis, we found four clusters that represented research conducted in North America (clusters 1 and 4), Europe (clusters 4, 6 and 7) and Australia (cluster 4). In the negative scores of the X-axis, we found one cluster of research conducted in Africa (cluster 2) and another in Asia (cluster 5). The second axis (Y-axis) represented a gradient between those studies that relied on social sciences (positive scores) versus natural sciences (negative scores) (Fig. 5). Whereas cluster 3 represented research that clearly belonged to social sciences, three clusters represented articles in the field of natural sciences (clusters 4, 6 and 7). Clusters 1, 2 and 5, which were located at intermediate positions on the axis, represented studies that applied more interdisciplinary approaches (Fig. 5).

The seven clusters represented research on different human-carnivore relations. Cluster 1 was comprised of articles focusing on the two species of bears in North America, U. arctos and U. americanus (78 papers), and therefore, it will be hereafter referred to as "North American bears". Cluster 2 represented a set of articles conducted in Africa about large carnivores, such as cheetah (Acinonyx jubatus), lion (P. leo), leopard (P. pardus), and spotted hyena (Crocuta crocuta) (69 papers; hereafter referred to as "African large carnivores"). Cluster 3 was comprised of articles that analyzed social aspects, such as opinions, beliefs, perceptions and attitudes expressed by different actors (mainly resident people and hunters) in relation to large carnivores in America (74 papers; hereafter called "Social research in America"). Cluster 4 included articles related to the feeding ecology of meso-carnivores, such as fox (Vulpes sp.) and weasel (Mustela sp.) in the Mediterranean region and Australia (53 papers; hereafter called "Meso-carnivores research"). Articles in cluster 5 focused on the impact of big felids, such as the tiger (P. tigris) and snow leopard (Uncia uncia), on the livelihoods of rural people in Nepal, Bhutan, India and China (118 papers; hereafter named "Asian felids"). Cluster 6 included studies about the impact of grey wolves (C. lupus) on livestock and natural prey, such as roe deer (Capreolus capreolus), red deer (Cervus elaphus) and reindeer (Rangifer tarandus), in the United States and Europe (54 papers; hereafter named "Conflicts with the grey wolf"). This cluster also included studies considering possible management options to mitigate the conflict with carnivores, such as economic compensation of damages, fencing and livestock husbandry. Finally, cluster 7 comprised articles dealing with the damages produced to human property by the raccoon (Procyon lotor), badger (Meles sp.) and bear (Ursus sp.) (56 papers; hereafter named

as "Damages to human property"). Key terminology identifying and characterizing each cluster according to the words' scores obtained in the detrended correspondence analysis is shown in Appendix G.

We found differences among the seven clusters regarding the

the lowest number. Finally, Meso-carnivores research also showed the lowest number of management recommendations and research on African large carnivores, Asian felids and Conflicts with grey wolf (clusters 2, 5 and 6, respectively) presented the highest number of
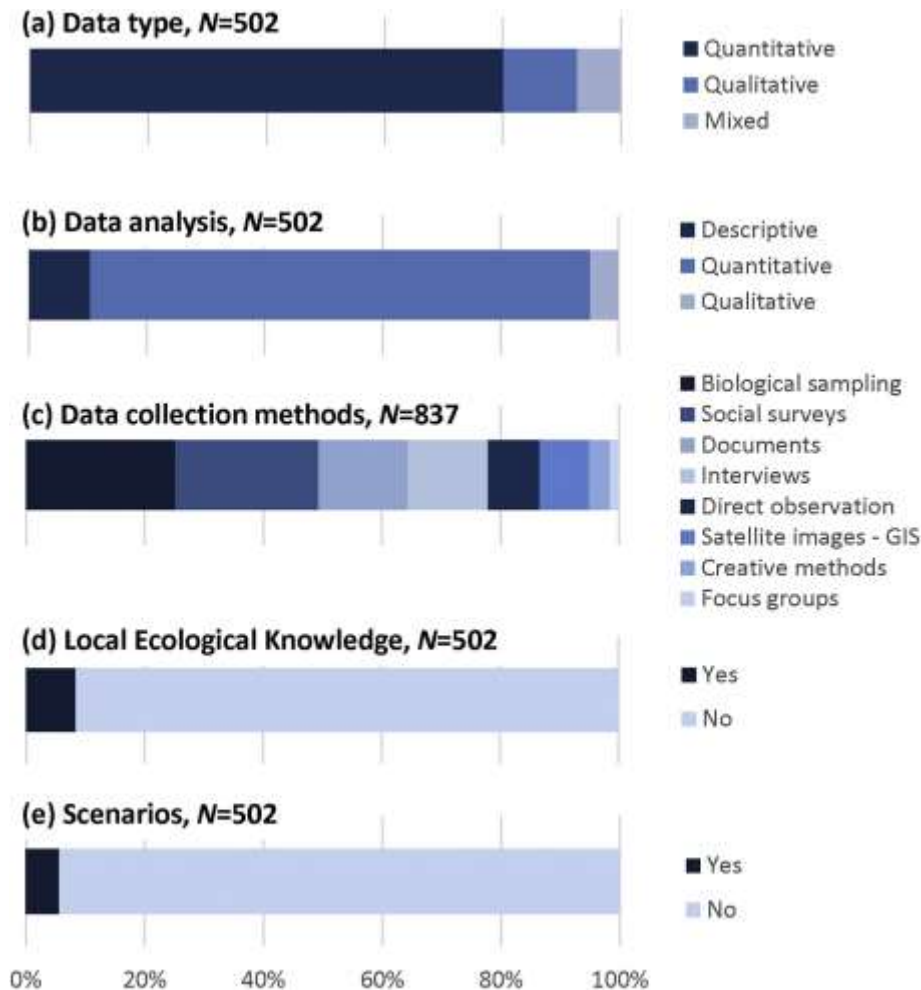

Fig. 4. Descriptive analysis of reviewed articles according to their methodological approach, including (a) data type, (b) type of analyses, (c) data collection methods, (d) consideration of local ecological knowledge as a source of information, and (e) application of scenario modeling and planning.

number of conflicts (Kruskal-Wallis test, H (6, N = 502) = 34.73, p < 0.001), ecosystem services (Kruskal-Wallis test, H(6, N = 502) = 20.15, p < 0.01), social actors (Kruskal-Wallis test, H(6, N = 502) = 29.19, p < 0.001), and management recommendations (Kruskal-Wallis test, H(6, N = 502) = 56.78, p < 0.001). By contrast, no difference among clusters was found for the number of drivers (Kruskal-Wallis test, H(6, N = 502) = 3.41, p > 0.1). First, while Meso-carnivores research and Conflicts with grey wolf (clusters 4 and 6) showed the lowest numbers of conflicts, the cluster on Social research in America (cluster 3) presented the highest number of conflicts. Regarding ecosystem services, Social research in America (cluster 3) represented the highest number of ecosystem services, whereas cluster 1 on North American bears represented the lowest number. The highest number of actors appeared in Social research in America (cluster 3), whereas Meso-carnivores research (cluster 4) considered

management actions. Statistics and graphs of the a posteriori multiple comparisons are shown in Appendix H.

4. Discussion

Since 2000 the absolute number of articles dealing with humancarnivore relations has continuously increased. This is probably a reflection of societies' growing interest in carnivore conservation but also related concerns arising from an increased number of human-carnivore encounters as well as massive declines in carnivore populations and geographic ranges (Linnell et al., 2001; Treves and Karanth, 2003; Wolf and Ripple, 2017). To understand how human-carnivore relations are shaped by current institutions and value systems, the emergence of influential social actors, and the result of changes in the carnivore communities, it is essential to develop management actions that foster coexistence between carnivores and

humans (Carter and Linnell, 2016; Chapron and López-Bao, 2016). However, we show that the available scientific literature is biased in different ways (e.g. geographical and taxonomic biases, more focus on conflicts than ecosystem services) and does not necessarily lead to an in-depth understanding of the socialecological properties underpinning human-carnivore relations.

The first bias we found was geographical. As previous systematic reviews of research in Conservation Biology and Ecology found (e.g., Fazey et al., 2005; Martin et al., 2012; Velasco et al., 2015; Nuñez et al., 2019), most studies were carried out in the Global North (Fig. 1b; Appendix D). This could be because less research is conducted in the Global South. However, because our systematic review was based on English-written articles, an inherent bias may exist towards studies conducted in countries with more capacity and resources for publishing in international English-language journals.

The geographical bias might entail that human-carnivore relations have been studied in few biomes, such as mountains, temperate forests and agro-systems. Although the underrepresentation of some biomes (e.g. polar areas or islands) could be explained because they host fewer carnivore species (Fig. 1d), our results showed that countries like Madagascar and biomes like tropical forests in the Global South (Fig. 1) presented lower number of articles than other biomes (e.g. temperate forests), despite these locations supporting a rich diversity of carnivores.

Finally, the geographical bias has also meant that research focuses primarily on species distributed in the Global North's biomes, such as the grey wolf, brown bear and American black bear. On the one hand, the underrepresentation of particular regions and biomes can lead to the underrepresentation of particular families (Fig. 1c). For example, the underrepresentation of studies that focus on species belonging to Eupleridae is associated with the fact that few studies were conducted in Madagascar (Fig. 1b). Nevertheless, a methodological limitation should be noted here since a more meaningful estimation of the expected number of studies per family (Fig. 1c) should refer to the respective damages and ecosystem services they deliver rather than the number of species belonging to each family. However, as this study also demonstrates, there is a clear knowledge gap on ecosystem services provided by carnivores and therefore, an accurate estimation of the expected number of studies for each biome is, as yet, not feasible. On the other hand, one might think that wolves and bears monopolize most of the research because they show very large ranges, so that the interface between humans and these carnivores would be large accordingly. However, there are a lot of species present in vast areas of Latin America, Africa and Asia (and even in the Global North), which have been not studied.

The body size of the species also appeared to influence the focus of the research. In fact, 70% of the articles were on large carnivore species (i.e. those weighting 15 kg or more; Bruskotter et al., 2017),
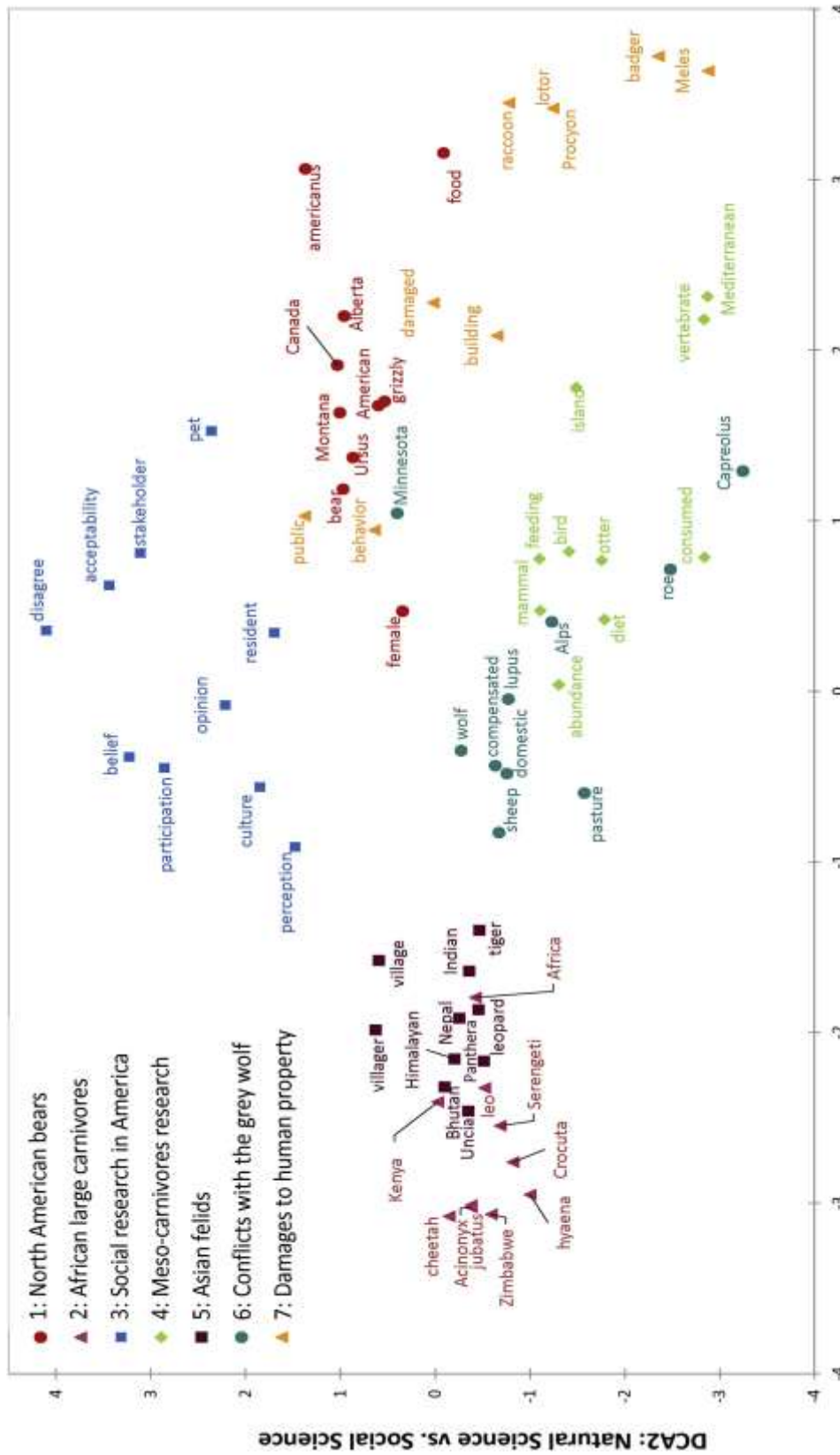
Fig.5. Results of the detrended correspondence analysis showing the seven clusters of research on human–carnivore relations with their representative words (differentiated by color and symbol), and their relations within the spaces shaped by both axes.

particularly wolves, bears and large felids (Brooke et al., 2014). In this sense, the majority of relations among humans and small or middlesized carnivores, such as those belonging to the families

Herpestidae, Mustelidae, Procyonidae and Viverridae, have received less scientific attention. The question suggested by these results is whether mesocarnivores are less studied than large carnivores

because they created less damage and provide lower levels of ecosystem services, or because meso-carnivores are less charismatic. Former research demonstrated that body size influences perceptions of species charisma (e.g. MartínLópez et al., 2008; Johnson et al., 2010), and that charisma also plays a role in selecting which species are the object of conservation research (e.g. Clark and May, 2002; Martín-López et al., 2009). Charisma seems to be the driving factor behind large carnivores receiving more scientific attention in human-carnivore relations research since there is evidence on the damages and ecosystem services provided by mesocarnivores. For example, spotted-necked otters (Lutra maculicollis) damage fishing equipment and take fish from fishermen in Benin (Akpona et al., 2015), and stone martens (Martes foina) frequently damage car engine components (Herr et al., 2009), both leading to conflicts. Mesocarnivores also provide important regulating contributions. Williams et al. (2018) found that mongooses and genets were essential to control rodents in the Vhembe Biosphere Reserve (South Africa), and Ćirović et al. (2016) demonstrated the relevance of the golden jackal (Canis aureus) in pest control and waste removal.

Numerous important human-carnivore relations occur in the less studied biomes of the Global South, as illustrated by the research clusters of African large carnivores and Asian felids (i.e., clusters 2 and 5; Fig. 5). Some of these relations are deeply intertwined with rural and indigenous lifestyles, in both positive and negative ways. For example, the Chenchu tribe in India depends on hunting and gathering in the forest, taking meat from big cats' prey while being tolerant about livestock losses to tigers and leopards, which are considered as if they were relatives (Reddy, 2010). By contrast, the Maasai people in Africa usually killed lions as a coming-of-age ritual, because of retaliation (linked to the warrior's duty) but also as a means of protest against national Governments (see Hazzah et al., 2013). Fortunately, the implementation of the Lion Guardians scheme in Kenya has been possible by changing the Maasai's system of values, by which young men currently gain social status through tracking and guarding lions (Hazzah et al., 2014). Human-carnivore relations, especially in southern Asia and Africa, also involve attacks (and sometimes kills) by large carnivores on humans, a circumstance that is much rarer in the Global North (Löe and Röskaft, 2004; McKay et al., 2018).

The current focus of research on conflicts in human-carnivore relations may inadvertently cause oversight of important beneficial relations between humans and carnivores derived through the provision of ecosystem services (Pooley et al., 2016). Beneficial contributions can be material, such as ornamental materials (Lindsey et al., 2013; Ripple et al., 2016); regulating, such as biological control (Ripple et al., 2014; Braczkowski et al., 2018; O'Bryan et al., 2018), seed dispersal (Cancio et al., 2017) and carcass removal (Moleón et al., 2014; Ćirović et al., 2016; Morales-Reyes et al., 2017); and non-material contributions, such as nature-based tourism (Maciejewski and Kerley, 2014; Willemen et al., 2015; Arbieu et al., 2018) and sacred experiences (Kellert et al., 1996; Herrmann et al., 2013).

To conceptualize human-carnivore relations primarily around conflicts could inadvertently perpetuate antagonism between wild carnivores and humans (e.g., Treves et al., 2006; Inskip and Zimmermann, 2009; Treves et al., 2016), which could further fuel negative attitudes towards carnivores (e.g. Kellert, 1985; Ericsson and Heberlein, 2003; Slagle et al., 2017). This might reinforce feedbacks between negative perceptions and the existence of conflicts, which may spur negative attitudes towards carnivores globally. Furthermore, neglecting the beneficial contributions of carnivores to human wellbeing in the scientific literature may jeopardize attempts to implement strategies that foster people's tolerance of carnivores and human-carnivore coexistence (Peterson et al., 2010; Pooley et al., 2016; Ceausu et al., 2018). To counteract existing biases in the current discourse, research on humancarnivore relations could fruitfully apply the concept of "nature's contributions to people" put forward by IPBES, which explicitly recognizes the dual role of biodiversity as provider of beneficial and detrimental contributions to people's wellbeing (Díaz et al., 2018).

In order to foster human-carnivore coexistence we must first understand the costs and benefits, but to so we need to understand the processes that drive these relations (Ceausu et al., 2018). Experts have already identified livestock predation, fear of carnivores, and mistrust between decision makers and locals among the most important drivers of conflict (Lute et al., 2018). However, human-carnivore relations are highly complex and determined by direct and indirect drivers that lead to shifts in social-ecological conditions at different scales, from local to global (e.g. Dickman, 2010; Lischka et al., 2018; Margulies and Karanth, 2018). Such fundamental shifts can be especially important because they can erode otherwise successful coexistence. In Transylvania, for example, local people considered coexistence with the brown bear to be relatively peaceful, but highlighted that especially changes in land-use (a direct driver) and bear management (an indirect driver) were eroding this coexistence (Dorresteijn et al., 2016). Despite the importance of the synergistic effect of multiple drivers of change in shaping human-carnivore relations, only 34.8% of articles considered multiple drivers.

In addition to the need of researching multiple drivers of change, future research should consider the existing telecoupled relations between drivers that influence human-carnivore relations. The application of the telecoupling framework (Liu et al., 2013) in human-carnivore research seeks to understand the interactions between socioeconomic and environmental components, among coupled social-ecological systems over distances that affect human-carnivore relations in a particular place. For example, an unprecedented level of conflicts due to livestock attacks between tigers and leopards and the villagers in the surroundings of Bandipur National Park (India) has recently been reported (Margulies and Karanth, 2018). Before 2005, the livelihood of local people in the surroundings of Bandipur relied on selling the dung of the native, low-maintenance cattle breeds to the nearby coffee plantations (Madhusudan, 2005; Margulies and

Karanth, 2018). The increasing global prices of coffee between 1990 and 2000 led to higher demand for dung in the coffee plantations, which also led to an increase in the number of cattle grazing inside Bandipur National Park. However, the decline of coffee prices in combination with the increasing costs of labor in 2005–2015 meant that coffee plantation owners used chemical fertilizers instead of cow dung. In addition, during the same period and due to forest overgrazing, the national park set a strict policy by which grazing was forbidden in the forest. As a result, between 2008 and 2013, the ownership of local cattle decreased by 34.9%, while the ownership of dairy cows, an expensive hybridised cattle, increased by 58.9% (Margulies and Karanth, 2018). This change also led to changes in the number of animals owned and the grazing system: while a villager owned a herd of animals of local cattle that grazed inside Bandipur, one villager can only own one or two dairy cows that are kept beside his home. With these changes, the level of human-carnivore conflict also rose because an attack to a dairy cow entails an important economic loss and an additional risk since the attacks happen inside the villages, while attacks to local cows in the forest were formerly considered an acceptable loss (Margulies and Karanth, 2018). The escalating conflict and declining tolerance to tigers and leopards around Bandipur National Park thus were the result of synergistic impacts of changes in the coffee global market and changes in the grazing policy of the national park, both indirect drivers that operate in different (and eventually distant) places. This example illustrates the need of an increased focus on the connection between multiple, sometimes tele-connected drivers of change.

Furthermore, as in other arenas of biological conservation (e.g. Bennett et al., 2017; Pooley et al., 2016), inter- and transdisciplinary research is needed to advance knowledge on human-carnivore relations and move forward coexistence (Pooley et al., 2016; Hovardas, 2018). As Echeverri et al. (2018) concluded after reviewing the research on human-animal relations, inter- and transdisciplinary approaches are crucial to identify innovative solutions to the pressing global challenges of wildlife conservation. In doing so, conservation scientists should engage with the social sciences and humanities, including with relevant theories and methods, such as qualitative, participatory, and arts-based approaches (Bennett et al., 2017; Echeverri et al., 2018; Hovardas, 2018). Because all methods have advantages and limitations, the use of multiple and mixed methods is widely recommended in the social sciences (Bennett et al., 2017). However, we found that research on human-carnivore relations remains strongly dominated by quantitative methods, while qualitative and participatory methods are much less applied (Fig. 4).

In addition, it has been recently recognized that in order to build impactful knowledge that contributes to effective conservation, scientists should include local ecological knowledge (Ban et al., 2018; Joa et al., 2018; Sobral et al., 2017). This idea of considering local ecological knowledge goes beyond science and is already recognized at the science-policy interface and in conservation policies (Díaz et al.,

2015; Tengö et al., 2017). Despite this recognition of local ecological knowledge elsewhere, its value for research on human-carnivore relations has been largely overlooked (Fig. 4). Most importantly, future research needs to better consider the local ecological knowledge of those actors who suffer directly the costs of human-carnivore encounters or who are engaged in the management of human-carnivore relations.

Management of human-carnivore relations is a controversial matter (e.g. Virgós et al., 2016; Lute et al., 2018). For example, the management strategies implemented in the Global North to mitigate humanpredator conflicts cannot be easily transferred to the Global South (e.g. Inskip and Zimmermann, 2009; Harihar et al., 2015). This review shows that most of the articles recommended management actions, although only 22% of articles actually evaluated their effectiveness (see Eklund et al., 2017; Holland et al., 2018; Moreira-Arce et al., 2018; van Eeden et al., 2018). Our results show that most articles mentioned nonlethal management actions, particularly the use of deterrents and barriers, husbandry techniques and livestock guarding (Fig. 3d), which have been proved effective to mitigate conflicts related with livestock attacks (e.g. Eklund et al., 2017; Moreira-Arce et al., 2018). Indeed, when several of these non-lethal measures are applied in combination, their effectiveness is much higher in preventing livestock attacks (Moreira-Arce et al., 2018), but also in fostering tolerance (Hovardas and Marsden, 2018). By contrast, the effectiveness of lethal management measures has not been shown to reduce livestock predation by carnivores (Treves et al., 2016; Eklund et al., 2017; Moreira-Arce et al., 2018), yet one third of the reviewed articles proposed it (Fig. 3d). Finally, education programs and economic incentives were frequently recommended in the reviewed literature. While the success of financial compensation has been mixed in fostering tolerance towards carnivores (e.g. Nyhus et al., 2003; Fernández-Gil et al., 2016), it seems that conflict mitigation is more likely to occur when non-lethal management measures, such as electric fences and guarding dogs, are a prerequisite for the payment (Bautista et al., 2017). Therefore, future research on human-carnivore relations should put more attention to integrated measures that include non-lethal control, education and compensation, as well as to evaluate their effectiveness in mitigating conflict and fostering coexistence.

5. Concluding remarks and future priorities

Our review showed there is increasing interest in studying humancarnivores relations through a social-ecological perspective. However, current research is biased geographically, taxonomically and methodologically, and has emphasized conflicts. To advance social-ecological research on human-carnivore relations, each of these biases should be rectified. A useful entry point to rectify these biases could be the recently proposed SEEDS framework put forward by Ceausu et al. (2018). Drawing on Ostrom's (2009) social-ecological systems framework in combination with the notion of ecosystem

services, the SEEDS framework recognizes four social-ecological system components – wildlife populations, the services and disservices for people arising from wildlife, governance arrangements, and different groups of people who are impacted by wildlife in different ways. Systematically disentangling these components across a wide range of geographic locations, species, and taking into account both benefits and disbenefits of wildlife could help to not only overcome the biases documented here, but also more generally pave the way towards more peacefully sharing the world with carnivores and other wildlife.

Deeply engaging with social-ecological systems, in turn, necessitates methodological pluralism (Fischer et al., 2015): facets such as the hidden costs of carnivore conflicts, deeply held cultural values attributed to carnivores, or the socially unequal distribution of the benefits and burdens of living with carnivores are unlikely to be captured adequately by conventional, quantitative techniques. Instead, interdisciplinary and transdisciplinary methods (which should be promoted in new Master and PhD programs), such as the development of shared mental models (Biggs et al., 2011), scenario planning (Peterson et al., 2003), or other stakeholder-oriented visioning techniques (Sharpe et al., 2016), may be helpful to navigate and resolve the real-world challenges of living with carnivores.

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Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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