REVIEW

Wild felids in trophic cascades: a global review

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Keywords
apex carnivore, ecosystem service, Felidae, green world hypothesis, interspecific interactions, mesocarnivore, mesopredator release, top predator, top-down

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Received: 29 July 2023
Accepted: 10 May 2024
Editor: RG

doi: 10.1111/mam.12358

ABSTRACT

1. Carnivores, often identified as keystone species, can influence prey and subordinate carnivores through density- and behaviourally mediated pathways. Although the magnitude of their impacts remains debated, carnivores may trigger successional direct and indirect ecological effects on lower trophic levels in specific contexts, commonly known as trophic cascades. Felids, as ambush predators, have great potential to impact food webs. Yet, their influence on ecosystem dynamics remains understudied.
2. This global comprehensive literature review aimed to assess evidence for felids' ecological roles in trophic cascades across both natural and human-dominated ecosystems.
3. We found 61 publications that studied the influence of 18 felid species in trophic cascades. Research exhibited taxonomic and geographic biases, favouring big cats, temperate regions and biomes, as well as tropical moist forests in Central and South America. Of the studies, 23% ($n = 14$) were experimental, while 77% were observational or correlative. Among the latter, 60% tested at least one alternative hypothesis and 47% examined bottom-up processes.
4. Despite varying levels of inference, 80% of studies provide information consistent with trophic cascades involving felids. Their examination confirmed wild cats' ability to induce density- and behaviourally mediated trophic cascades, thereby influencing critical biotic and abiotic processes, including mesopredator control, functional diversity maintenance, and carbon storage. The magnitude of these effects may be altered in human-dominated landscapes, although current research effort remains too limited to draw conclusions.
5. In conclusion, felids may act as drivers of ecosystem change, and acknowledging their ecological roles can aid in promoting their conservation. However, we encourage more strongly inferential and comprehensive investigations into felid-mediated trophic cascades, prioritising research on small cats, felids in Asia and Africa, and the impacts of humans on trophic cascades, which can help to better inform conservation interventions and perspectives.

INTRODUCTION

Carnivores are key components of functional ecosystems, being involved in intricate interactions among a diverse array of species (Estes et al. 2011). They frequently serve as keystone species, playing pivotal roles within ecosystems (Ritchie et al. 2012, Ripple et al. 2014). Authors employ differing criteria to categorise this taxonomic group, based on body size, classifying carnivores as large (>20 kg), and small (<20 kg) (Carbone et al. 2007, Marneweck et al. 2022), or their trophic positions, distinguishing apex carnivores (i.e. top-level) from mesocarnivores (i.e. subordinate carnivores) (Prugh & Sivy 2020). The impacts of carnivores on their prey and subordinate counterparts can be significant and be expressed through mechanisms such as predation, avoidance, competition and facilitation (Prugh et al. 2009, Ritchie et al. 2012, Saggiomo et al. 2017). However, these impacts are highly context-dependent, and are influenced by carnivores' specific traits (e.g. body mass, diet, hunting strategy), environmental factors (e.g. seasonality, primary productivity), and other variables (e.g. intraguild interactions, level of anthropisation) (Haswell et al. 2017). Despite the intricate nature of interspecific interactions shaping global food webs, researchers have strived for a deeper understanding of these dynamics, and the factors influencing them (Estes et al. 2011). This has led to the rise of the ecological concept of 'trophic cascades', defined as successional impacts of predators on lower trophic levels propagating downward through food webs (Terborgh & Estes 2010, Ripple et al. 2016b). Although a growing body of evidence supports this concept in the scientific literature, its quality remains contentious due to concerns about the inferential strength and the robustness of the methods used (Allen et al. 2017a, Castle et al. 2023, Hobbs et al. 2024).

The original hypothesis stemming from the 'trophic cascade' concept suggests that carnivores control herbivores, which facilitates vegetation regeneration, and the absence of this limitation causes plant damage from an increase in the populations of primary consumers (i.e. 'green world hypothesis'; Hairston et al. 1960). Beyond 'density-mediated cascades' (consumptive effects), carnivores may also trigger 'behaviourally mediated cascades' (non-consumptive effects) by creating a 'landscape of fear' through their simple presence and cues (Schmitz et al. 1997, Laundré et al. 2010, Suraci et al. 2016). In response, some prey and subordinate carnivores adapt their behaviour, diet, activity patterns, and spatial distribution to optimise the trade-off between predation risk and food acquisition, thereby influencing their fitness (Preisser et al. 2005, Gaynor et al. 2019, LaBarge et al. 2022). Even though smaller carnivores do not usually account for large shares of apex carnivore diet, mechanisms such as avoidance and intraguild killing may also represent strong top-down controls (Palomares & Caro 1999, Prugh & Sivy 2020). Intraguild interactions are increasingly recognised as crucial to visualise the food web more realistically (Prugh et al. 2009, Welch et al. 2022). According to the 'mesopredator release hypothesis' (Crooks & Soulé 1999), losses of large carnivores could lead to outbreaks of subordinate carnivores and/or to behaviourally mediated cascades, resulting in increased predation on smaller prey that are seed-dispersers or seed-predators, which in turn could influence fauna-flora interactions (Ritchie & Johnson 2009, Roemer et al. 2009, Haswell et al. 2017).

For these reasons, carnivores, in particular the largest, are widely recognised for their capacity to exert far-reaching impacts, indirectly influencing ecosystem functions and services, including carbon storage (Beschta & Ripple 2019), biodiversity maintenance (Estes et al. 2011, LaBarge et al. 2022), nutrient cycling (Schmitz et al. 2010, Morris & Letnic 2017, Monk & Schmitz 2022), control of invasive species (Ripple et al. 2014), and disease regulation (Brashares et al. 2010, Levi & Wilmers 2012).

Identifying direct and indirect impacts of carnivores within food webs remains particularly challenging (Ford 2015, Montgomery et al. 2019). While researchers often argue for their strong top-down effects on lower trophic levels, relying predominantly on correlations, causation often remains unproven (Ford & Goheen 2015, Allen et al. 2017a, b). Consequently, extensive research on the influence of iconic carnivores on their respective ecosystem has faced scrutiny in the scientific community, highlighting methodological limitations and interpretation biases in existing literature (e.g. Hayward et al. 2015, Castle et al. 2023 on dingoes (*Canis dingo*) in Australia and Kauffman et al. 2010, Hobbs et al. 2024 on grey wolves (*Canis lupus*) in Yellowstone). Beyond the accuracy of some sampling techniques and the robustness of certain experimental designs, several scientists have denounced a general oversight of alternative hypotheses to top-down effects (e.g. Allen et al. 2017a, Hobbs et al. 2024). As these effects are highly context-specific, they necessitate evaluation alongside other potential causal factors, such as bottom-up effects, and require strongly inferential experiments to assess causal processes (Haswell et al. 2017, Allen et al. 2017b). Yet, such experiments remain particularly rare given their cost and the difficulty of implementing them in the field (Ritchie et al. 2012, Ford & Goheen 2015). Caution and nuanced interpretations have thus been recommended when reporting the findings of observational and correlative studies (Haswell et al. 2017, Allen et al. 2017a, Hobbs et al. 2024).

Despite the Felidae being among the most iconic carnivores around the globe, their influence on food webs has received little attention (Kuijper et al. 2016, Moll et al. 2017). Yet, felids appear to have great potential to significantly impact lower trophic levels, warranting interest in exploring their ecological roles within ecosystems (Elbroch et al. 2017). Felidae – comprising 41 species (Table 2) – are the only Carnivora family composed exclusively of hypercarnivorous species. They include the highest number of large carnivore species (Ripple et al. 2014), and exhibit the most highly specialised predator morphology among carnivores (Castelló 2020). Furthermore, felids are mostly solitary and stalking predators (Carbone et al. 2007), which may amplify their predator–prey interactions, as they tend to induce stronger risk effects, to have higher kill rates and to provide more carrion to scavenging communities than other carnivores (Preisser et al. 2007, Elbroch & Wittmer 2012, Allen et al. 2014). Occupying a wide range of habitats and ecological niches around the world, felids' impacts are likely to differ from one ecosystem to another, and from large to small species (Castelló 2020, LaBarge et al. 2022). Although less studied, smaller wild cats might also play significant roles in food webs (Roemer et al. 2009, Marneweck et al. 2022).

This review examines the quality and quantity of available evidence regarding the ecological impacts of felids in trophic cascades across both natural and human-dominated ecosystems globally. It provides a comprehensive assessment of our current understanding, outlining both strengths and limitations in existing research. Emphasising the identified gaps in knowledge, the review advocates for further experimental studies. A deeper comprehension of the roles felids play in functional ecosystems necessitates additional investigations that could be used to better understand the potential outcomes of restoration programs. Recognising the ecological arguments of felid roles within ecosystems, this review underscores the importance of such insights in supporting other claims for conservation actions, thereby contributing to the implementation of effective interventions.

METHODS

A literature search was conducted in two databases: 1) Scopus, which is a 'repeatable single resource' recommended for systematic reviews (Haddaway et al. 2022), and 2) the IUCN/SSC Cat Specialist Group library (http://www.catsg.org/catsglib/index.php), which contains peer-reviewed articles specific to felids. To identify studies, we combined two distinct sets of search terms in Scopus. The first one included the scientific and English names of the 41 felid species (Castelló 2020), along with the terms 'felid' and 'wild cat'. The second set included the following string of keywords referring to trophic cascades: 'trophic', 'cascade', 'top-down', 'food web', 'Green World Hypothesis', 'Mesopredator Release Hypothesis', 'apex', 'mesocarnivore', 'mesopredator', 'ecology of fear', 'landscape of fear', 'predation risk', 'non-consumptive' and 'ecosystem service'. Since the IUCN/SSC Cat Specialist Group library only contains literature on felids, only the second set of keywords was used for the search. The literature was reviewed until December 2022, and no early date limit was set.

Based on titles and abstracts, we retained empirical studies focusing on trophic cascades worldwide, involving three or more trophic levels and including at least one felid species, except the feral cat (*Felis catus*), considered non-native in most ecosystems. Research that exclusively addressed predator–prey or intraguild interactions without explicitly quantifying the impact they might have on a third component of the food web were not considered. However, if an author combined two of their papers to identify a trophic cascade, or addressed the same trophic cascade (with exactly the same trophic levels involved) in several papers, they were all considered but counted as one single study in the results. After screening the outputs from both databases for each felid species, the 'snowball technique' (Livoreil et al. 2017) and the 'Research Rabbit' application (https://researchrabbitapp.com) were used to find additional relevant publications by looking at the references of the selected papers and the citation network to which they belonged, respectively.

To identify existing knowledge and research gaps, we recorded for each study the species/groups of species involved in the trophic cascade, the cascading impacts (positive, negative or neutral) within the food web, their type (i.e. density-mediated or behaviourally mediated), the geographic coordinates and the environmental context of the study site, the methodological approach used, and whether the study reported identifying a trophic cascade. The environmental context of the study site (i.e. well-preserved vs. degraded) was defined using the decision tree presented in Appendix S1. For the methodological approach, we categorised studies into five groups (Table 1), adapted from Ford and Goheen (2015), to assess the inferential evidence presented by each individual study. We also examined whether studies tested for alternative hypotheses (e.g. bottom-up impacts), recognising that this aspect significantly influences the overall quality of evidence presented in a paper.

We classified each documented trophic cascade into one of the following categories, based on the main mechanism by which the cascade was initiated: 1) classic (stemming from shifts in apex carnivore-prey interactions), 2) intraguild (stemming from shifts in apex carnivore-mesocarnivore interactions), 3) human-induced (stemming from shifts in human-apex carnivore interactions in a system where humans and felids co-occur) (Fig. 1).

Table 1. Definition of the five methodological approaches identified in reviewed papers and used to determine whether a trophic cascade is occurring in the system studied. The approaches are ranked in ascending order of level of inference and adapted from the classification developed by Ford and Goheen (2015)

Approach	Definition
Hypothetical	*Observational studies*, assuming one or more interspecific interactions in the cascade rather than measuring them and/or relying on non-robust presence/absence data for the top trophic level
Spatial	Correlative studies using *spatial comparisons* between diverse sites or landscape areas characterised by varying levels of felid abundance to investigate ecological interactions within trophic levels
Temporal	Studies using *time series* from a *singular locality* to analyse species abundance across trophic levels and assess continuous correlations over a specific time period
Spatiotemporal	Correlative studies using *time series* on species abundances *across diverse sites* with varying levels of felid abundance, *including a control site* devoid of felids, to investigate the role of top-down control on lower trophic levels
Experimental	Manipulative studies employing *replicated field experiments*, including *paired control and tested treatments*, manipulating food chain length or predation risk (e.g. through exclosures or simulated cues of presence) to isolate and quantify the effect of top-down forces among other ecological processes

We also assessed whether the spatial distribution of research studies accurately reflected the terrestrial biomes found within the global range of felids through an exact multinomial test (LaBarge et al. 2022). We used the packages *sf*, *raster*, and *fasterize* in RStudio version 2023.06.0 to rasterise the updated version of the *Terrestrial Ecoregions of the World* shapefile (Dinerstein et al. 2017), and to assign corresponding biomes to study sites. Subsequently, we determined the distribution of felid species among biomes found within the global range of felids by 1) aggregating felid distribution data from the IUCN Red list (2022) (all available data except for polygons designated as 'extinct' or 'possibly extinct'), 2) calculating its overlap with each biome, and 3) weighting biomes based on the number of felid species present in each polygon, creating a 'cumulative' biome distribution within the global range of felids.

RESULTS AND DISCUSSION

Our systematic review identified 61 publications meeting our eligibility criteria relative to the role of felids in trophic cascades (Appendix S2). Publication dates ranged from 1984 to 2022, with 57% of the studies published over the last decade. The low number of publications over such a long period of time could be due to the complexity of the subject, which requires the mobilisation of a wide range of expertise in various taxa. Alternatively, this increase could have been driven by a recent surge in interest in large carnivore and trophic cascade research, coupled with significant technological advancements in monitoring cryptic and low-density species such as felids, thereby providing new research opportunities.

Studied wild cat species and body size

Only 14 out of the 41 felid species considered were documented as being part of a trophic cascade (Table 2). By far, the most studied cat species in trophic cascades were the puma (*Puma concolor*) (46%, $n=28$), followed by the leopard (*Panthera pardus*) (16%, $n=10$), and the jaguar (*Panthera onca*) (16%, $n=10$). In general, the puma stands out as the most extensively studied felid species in the scientific literature (Brodie 2009). It has the widest latitudinal distribution of any wild terrestrial mammal (Castelló 2020, LaBarge et al. 2022) and has benefited from extensive research in North America over the past two decades (Beschta & Ripple 2009, LaBarge et al. 2022). Our review also included 11 smaller felid species, such as the bobcat (*Lynx rufus*) (16%, $n=10$), the ocelot (*Leopardus pardalis*) (11%, $n=7$), and the Iberian lynx (*Lynx pardinus*) (5%, $n=7$). The bobcat is one of the most abundant and investigated medium-sized carnivores in North America (Dyck et al. 2022). Similarly, the ocelot is the second most studied small cat species worldwide (Brodie 2009), whereas the Iberian lynx has garnered significant conservation efforts and research due to its IUCN listing as Critically Endangered from 2002 to 2015 (Palomares et al. 2011).

Large felids have received the most attention for their role in trophic cascades. Taken together, they were associated with 82% of the reviewed studies ($n=50$). Increasing mammalian biomass generally correlates with a commensurate rise in research efforts dedicated to studying these species (Ripple et al. 2016a). Numerous studies, including ours, confirmed that this trend extends to big cat species, which are studied more often than smaller felid species, owing to the endangered and/or emblematic status of big cats, as well as their history of conflict with humans (Ripple et al. 2014, Lozano et al. 2019). Additionally, their large size is often associated with their ability to shape ecosystems with far-reaching effects on lower trophic levels, a role that smaller carnivores cannot fulfil, some argue (Wallach et al. 2015, Avrin et al. 2023). In this review, the snow leopard (*Panthera uncia*) is the only big cat for

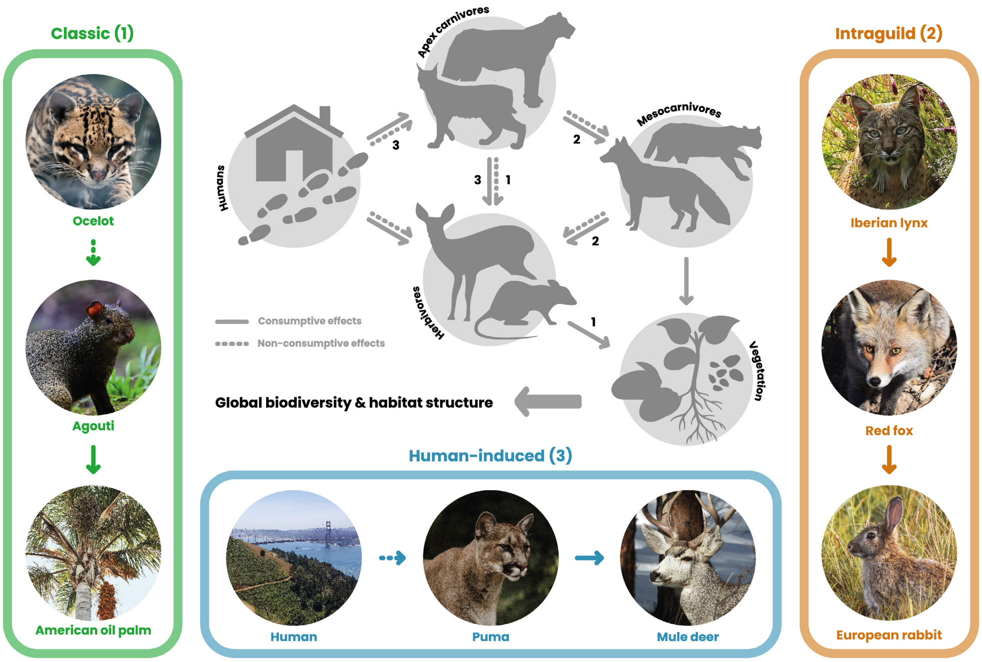

Fig. 1. Conceptual framework illustrating the different types of trophic cascades that may result from complex trophic interactions among apex carnivores, mesocarnivores, herbivores, vegetation, and humans, and shaping biodiversity and habitat structure in global ecosystems. Examples of each type of trophic cascade involving a felid species are depicted in boxes. Classic, in green: the fear effect induced by the ocelot (*Leopardus pardalis*), the apex carnivore in this system in Panama, reduced seed dispersal of *Attalea butyracea* by agoutis (*Dasyprocta punctata*) (Gálvez & Hernández 2022). Intraguild, in orange: the recovery of Iberian lynx (*Lynx pardinus*) populations in Spain was intricately correlated with a reduction in red fox (*Vulpes vulpes*) abundance, and a concurrent increase in European rabbit (*Oryctolagus cuniculus*) populations, as revealed by a quasi-experimental design (Jiménez et al. 2019). Human-induced, in blue: Pumas (*Puma concolor*) were shown to avoid areas close to human settlements in the county of Santa Cruz (USA), creating a refuge for mule deer (*Odocoileus hemionus*) populations, which altered vegetation structure due to increased browsing intensities (Yovovich et al. 2021). The numbers assigned to each type of trophic cascade (i.e. 1, 2 or 3) are repeated in the central diagram to indicate the type of trophic cascade each arrow represents. Photography (from left to right, top to bottom) © D. van de Sande, B. Weckx, S. Noël, B. Morris, P. Du Preez, C. Greene, O. Guder, J. Snoek & Pixabay.

which no result was found. Yet, this cryptic species is often represented in other research topics, such as human-wildlife conflicts (Rashid et al. 2020) and population monitoring (Janečka et al. 2011). The mountainous landscapes of central Asia in which the snow leopard and its prey live are particularly rugged, inaccessible and challenging to work in, which is likely to limit the opportunities to study complex processes such as trophic cascades. Furthermore, these low-resource areas (low prey densities and sparse vegetation) would necessitate a substantial sampling effort to uncover potential trophic cascades.

Geographical trends and biases

The global distribution of studies encompassed 24 countries, highlighting significant disparities in spatial coverage across felids' range (Fig. 2). The ecological role of wild cats in trophic cascades has predominantly been studied in the northern hemisphere, with a particular emphasis on the United States, although only five wild felids are extent in this country. This geographical bias reflects a recurring pattern within the fields of ecology and conservation (Pyšek et al. 2008, Trimble & van Aarde 2012, Hickisch et al. 2019). Multiple factors contribute to these geographic disparities, including political instability, limited access, infrastructure and resources, lower conservation investments, and reduced scientific means in the Global South (Hickisch et al. 2019, Strampelli et al. 2022). The United States also mirror a depauperate post-Pleistocene fauna arising from the Pleistocene megafaunal extinctions (Malhi et al. 2016, Fricke et al. 2022). Ecosystems with simpler trophic chains showcase lower ecological complexity, functional redundancy, and thereby, resilience, which may result in more pronounced cascading effects in such ecosystems (Smith et al. 2022).

Similarly, the distribution of studies across biomes did not align with expectations based on the cumulative geographic range of all felid species (exact multinomial test, $P < 0.0001$; Fig. 3). Whereas felid species hotspots are concentrated in tropical ecosystems, our results indicate

Table 2. List of the world's felid species, sorted by decreasing average body mass (ABM) based on data from Castelló (2020), with their IUCN status (i.e. 'Least Concern' [LC], 'Near Threatened' [NT], 'Vulnerable' [VU] or 'Endangered' [EN]). The table presents the total number of studies that have documented trophic cascades (TC; highlighted in grey) involving at least three trophic levels, for each felid species, categorised by the category of TC (i.e. 'classic' [C], 'intraguild' [I], 'human-induced' [H]). The number of studies out of the total for which the data were inconclusive, or top-down effects could not be observed, are shown in parentheses

				Nb. of studies with TC documented			
Species name		ABM (kg)	IUCN	C	I	H	Total
Lion	*Panthera leo*	151.8	VU	2 (1)	2 (1)	1	5 (2)
Tiger	*Panthera tigris*	138.0	EN	2	4	0	6
Jaguar	*Panthera onca*	82.5	NT	5 (1)	4 (2)	1	10 (3)
Puma	*Puma concolor*	52.4	LC	8 (1)	10 (2)	10 (1)	28 (4)
Leopard	*Panthera pardus*	42.7	VU	4	6 (1)	0	10 (1)
Snow leopard	*Panthera uncia*	42.3	VU				0
Cheetah	*Acinonyx jubatus*	38.6	VU	1	0	0	1
Eurasian lynx	*Lynx lynx*	22.4	LC	4 (1)	1	3 (2)	8 (3)
Sumatran/Bornean clouded leopard	*Neofelis diardi*	17.5	VU				0
Indochinese clouded leopard	*Neofelis nebulosa*	14.8	VU				0
Caracal	*Caracal caracal*	11.2	LC	0	(1)	0	(1)
Serval	*Leptailurus serval*	10.5	LC				0
Iberian lynx	*Lynx pardinus*	10.2	EN	0	3	0	3
Ocelot	*Leopardus pardalis*	10.0	LC	2	3 (2)	2	7 (2)
Asiatic golden cat	*Catopuma temminckii*	9.9	NT				0
Canada lynx	*Lynx canadensis*	9.3	LC	(1)	0	0	(1)
Fishing cat	*Prionailurus viverrinus*	9.2	VU				0
African golden cat	*Caracal aurata*	9.1	VU				0
Bobcat	*Lynx rufus*	8.8	LC	4 (2)	4	2	10 (2)
Jungle cat	*Felis chaus*	7.8	LC				0
Chinese mountain cat	*Felis bieti*	7.3	VU				0
European wildcat	*Felis silvestris*	5.5	LC				0
Jaguarundi	*Herpailurus yagouaroundi*	5.3	LC	0	1 (1)	1	2 (1)
African/Asian wildcat	*Felis lybica*	5.0	LC				0
Andean mountain cat	*Leopardus jacobita*	4.8	EN				0
Geoffroy's cat	*Leopardus geoffroyi*	4.2	LC	0	0	1	1
Bay cat	*Catopuma badia*	4.0	EN				0
Marbled cat	*Pardofelis marmorata*	3.8	NT				0
Margay	*Leopardus wiedii*	3.4	NT	0	1 (1)	1	2 (1)
Pallas's cat	*Otocolobus manul*	3.4	NT				0
Leopard cat	*Prionailurus bengalensis*	3.4	LC				0
Colocolo	*Leopardus colocolo*	3.0	NT	0	0	(1)	(1)
Southern tigrina	*Leopardus guttulus*	2.8	VU	0	0	1	1
Eastern tigrina	*Leopardus emiliae*	2.4	VU				0
Northern tigrina	*Leopardus tigrinus*	2.4	VU	0	(1)	0	(1)
Sunda leopard cat	*Prionailurus javanensis*	2.2	LC				0
Guiña	*Leopardus guigna*	2.1	VU				0
Sand cat	*Felis margarita*	2.0	LC				0
Flat-headed cat	*Prionailurus planiceps*	1.9	EN				0
Black-footed cat	*Felis nigripes*	1.7	VU				0
Rusty-spotted cat	*Prionailurus rubiginosus*	1.4	NT				0

a bias towards several temperate biomes, including 'Mediterranean Forests, Woodlands, and Scrub', as well as temperate broadleaf and coniferous forests. However, the high occupancy of felids in 'Tropical and Subtropical moist broadleaf forests', which constitutes 23% of the cumulative felids' range, aligns with the proportional representation of this biome in our study (26%). Yet, the studies included in this category primarily focused on the forests of Central and South America ($n=11$ studies), while tropical forests in South-East Asia ($n=4$ studies) and Africa ($n=1$ study) remain poorly studied compared to the number of felid species they encompass. For example, we recorded no study in Central Africa despite this region containing the second largest basin of tropical forests in

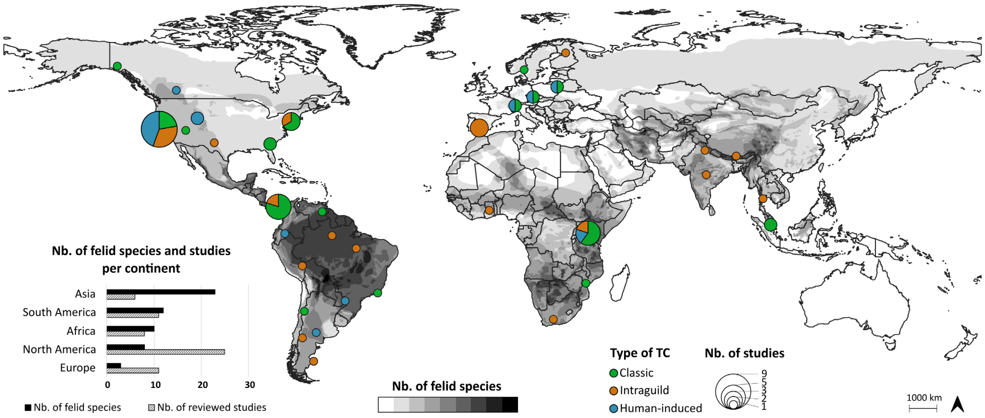

Fig. 2. Spatial distribution of felid species and reviewed studies. Study sites are represented by dots or pie charts when multiple studies are grouped together by region (size proportional to the number of studies), with a colour code indicating the type of trophic cascade (TC) studied.

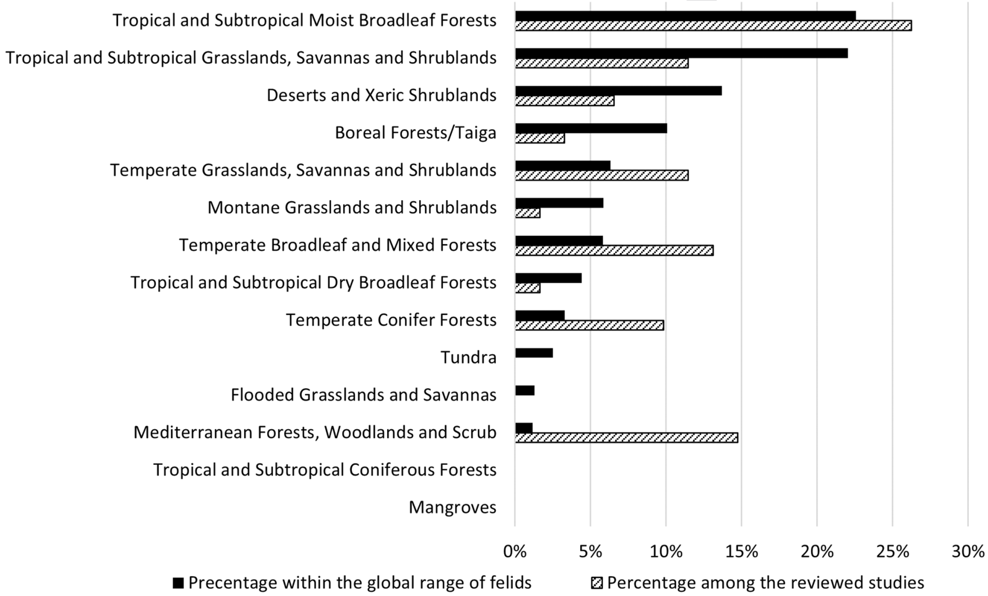

Fig. 3. Representation of biomes within the global range of felids and in reviewed studies.

the world, and the magnitude of top-down effects induced by carnivores appears to be particularly important in productive environments (Hoeks et al. 2020).

Our findings, along with recent review papers on pumas (LaBarge et al. 2022), lions (*Panthera leo*) (Visser et al. 2023), and leopards (Jacobson et al. 2016), highlight the global imbalance in geographic coverage of research attention in addressing knowledge gaps and conservation needs for felid species.

Quality of evidence

The strength of causal inference (hereafter, 'inference') regarding the ecological role of felids in trophic cascades varied greatly across the reviewed studies (Fig. 4), contingent upon factors such as the experimental design approach, the replication rate, the spatiotemporal coverage, the applied survey methods, and the incorporation of covariates or control elements for testing or controlling for alternative hypotheses (Allen et al. 2017a).

A quarter of the studies based on highly hypothetical assumptions had a particularly low level of inference, and were, thus, not developed further in our review. The four other methodological approaches (i.e. spatial, temporal, spatiotemporal and experimental) were used in 33%, 11%, 8% and 23% of the reviewed studies, respectively. Within the spatial category, some studies had a stronger inference than others, depending notably on the number of sites

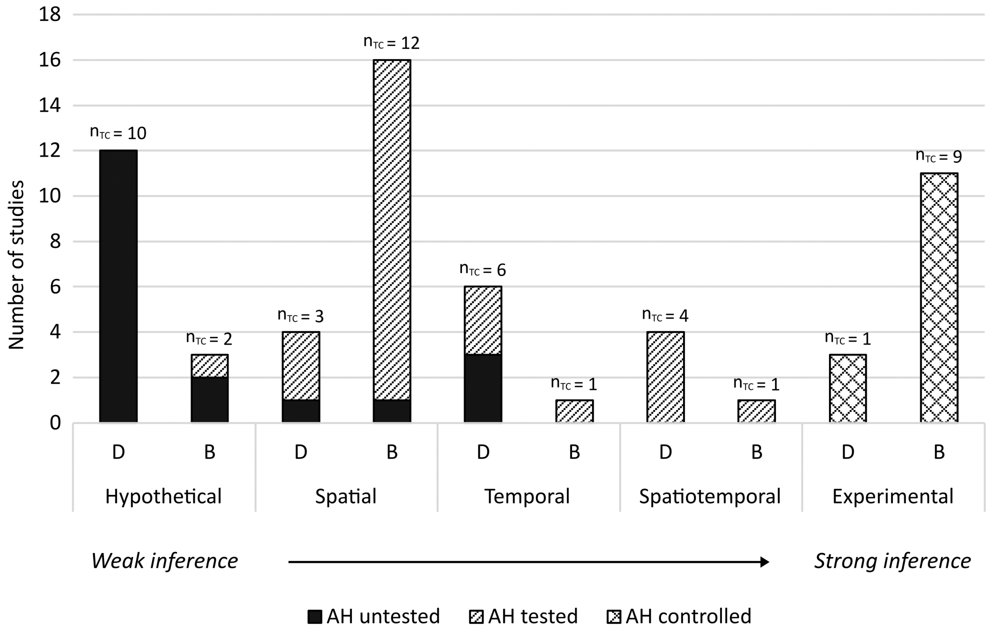

Fig. 4. Number of studies according to the five different methodological approaches, the type of cascading effects tested (i.e. 'density-mediated' [D] or 'behaviourally mediated' [B]) and 'untested / tested / controlled for alternative hypotheses' (AH), with the number of studies considered to have identified a trophic cascade (n_{TC}) indicated above each bar.

and the total area surveyed, ranging from 15 km^2 (Palomares et al. 1995) to 3800 km^2 (Cruz et al. 2018). Time series are statistically and methodologically more powerful for testing a carnivore-mediated trophic cascade than the spatial approach, which is more likely to confound the impact of the felid species with other variables (Ford & Goheen 2015). However, obtaining time series data requires long-term surveys, which are resource-intensive, and the ability to predict where and when local felid populations will change (Ripple et al. 2014).

An alternative approach is to combine multiple field experiments to study interactions under controlled and replicated conditions, as was done in 14 studies. For 'classic' cascades, combining telemetry or camera trap data with herbivore exclosures or vegetation monitoring in felid-rich and felid-poor areas is a robust option (e.g. Ford et al. 2014, Gálvez & Hernández 2022). Alternatively, the absence/presence of felids can be experimentally manipulated by simulating a landscape of fear with scent or auditory cues (e.g. Atkins et al. 2019, van Beeck Calkoen et al. 2021). This approach can demonstrate the potential non-consumptive effects of wild cats, which can be a quick and effective way of highlighting prey or competitor behavioural responses and thereby, a potential trophic cascade if coupled with the monitoring of indirect effects (Ritchie et al. 2012, Suraci et al. 2016). Our findings indicate a higher prevalence of robust evidence for behaviourally mediated trophic cascades compared to density-mediated ones, probably due to the more manageable conditions for replication and control, even though certain parameters of the experimental design need to be carefully considered (see Prugh et al. 2019). Results from these behaviourally mediated trophic cascades indicate that felids cause avoidance in prey and mesocarnivores, but do not demonstrate potential long-term effects on demographic trends. Yet, other studies have shown that carnivore-induced behavioural changes could affect survival rates (Preisser et al. 2005, Sheriff et al. 2009), leaving the question open for wild cats.

Although manipulative studies offer the advantage of robust inferences (Paine 1980, Polis & Strong 1996), their implementation faces considerable challenges with felids, given their large size, long lifespan, and high mobility (Estes et al. 2011), leading to the predominance of non-experimental approaches in 77% of studies. These may still provide valuable insights into the ecological functions of felids within ecosystems, but their reliability depends on the thorough examination of alternative hypotheses to demonstrate whether top-down control is the true causal agent responsible for changes in both direct and indirect species interactions (Ford & Goheen 2015, Allen et al. 2017b).

In this review, 60% of the observational and correlative studies ($n = 28$) actively explored at least one alternative hypothesis, while 40% ($n = 19$) did not investigate potential counteractive data. In some cases, bottom-up effects may better explain the overabundance of herbivores rather than the loss of apex carnivores (Palmeirim et al. 2021). Similarly, the high productivity of some habitats, which enables plants to regrow quickly, may compensate for herbivory, making it challenging to identify top-down effects (Donadio & Buskirk 2016). However, among the 22 studies that investigated bottom-up factors, 10 identified stronger top-down effects, only one found weaker top-down effects, and 11 reported that the observed phenomena emanated from the interplay of both top-down and bottom-up processes.

These results highlight the inherent complexity when studying such ecological mechanisms shaped by species assemblages, spatiotemporal factors, and ecosystem characteristics. For example, variations in climate conditions and alternative sources of predation have potentially led to a distortion of the role played by pumas in Zion National Park in the USA (Ripple & Beschta 2006). Conversely, Donaldson et al. (2022) found that the intricate and reticulated food webs, as evident in some African savannas, appear to dampen top-down effects throughout the food chain, attenuating the influence of apex carnivores on basal trophic levels.

Ecological roles of felids in trophic cascades

Out of the 61 studies we reviewed, 25 were classified as ‘classic’ (41%), 22 as ‘intraguild’ (36%) and 14 as ‘human-induced’ (23%) trophic cascades (Appendix S2). Most studies (80%, $n=49$) asserted to have identified a trophic cascade. Their examination provided valuable insights into the diverse ecological roles that felids, through density- and behaviourally mediated trophic cascades, may indirectly play in major biotic and abiotic mechanisms, such as mesopredator control, maintenance of functional diversity, and carbon storage.

To conscientiously address the experimental design limitations outlined above, terms in subsequent sections have been carefully selected to align with the strength of inference in the detailed examples. Notably, terms like ‘evidence’, ‘experimental’, and ‘demonstrate’ are exclusively employed for case studies derived from the 14 studies classified as experimental in the previous section – these being the closest to offering concrete evidence for causal relationships. For further information, the characteristics and key findings of these specific studies are highlighted in Appendix S2.

CLASSIC TROPHIC CASCADES

By controlling granivore, frugivore and herbivore populations, felids have been reported in the reviewed studies to limit seed predation, browsing, grazing and/or trampling intensity, thereby promoting seed dispersal and seedling establishment in given contexts (Terborgh et al. 2006, van Beeck Calkoen et al. 2021, Burgos et al. 2022). The positive (95%, $n=18$) and negative (5%, $n=1$) indirect roles of 10 felid species on vegetation regeneration have been identified in 19 reviewed trophic cascades. The intermediate trophic level through which felids indirectly affected plants was mostly ungulates ($n=12$), followed by rodents ($n=3$), mixed taxa ($n=3$) and, in one case, an herbivorous monkey (i.e. the black capuchin monkey *Sapajus nigritus*).

Our results show that the puma is the most studied felid species supporting the ‘green world hypothesis’, as interpreted by the authors ($n=7$). While four of these studies had the lowest inferential power, Donadio and Buskirk (2016) provided strong evidence linking low puma predation risk and abundance with released vicuña (*Vicugna vicugna*) pressure on herbaceous vegetation in Argentine steppes. More recently, puma predation has also been correlated with increased canopy cover in Arizona wetlands by reducing donkey (*Equus africanus*) stress on plants and soil (Lundgren et al. 2022).

Where the apex carnivores have disappeared and trophic chains are truncated, herbivory can become so intense that it can cause drastic shifts in plant communities (Estes et al. 2011, Ripple et al. 2014). Island systems helped to support this theory, such as the artificially formed tropical forested Lago Guri islands in Venezuela, where some pioneer studies took place: Terborgh et al. (2001, 2006) concluded using a replicated space-for-time approach that the absence of jaguars and pumas on these islands has resulted in a substantial transformation of the plant community, primarily driven by the intensification of seedling herbivory by generalist herbivores. Conversely, the translocation of bobcats to a previously predator-free island in Georgia, USA, was correlated with a significant increase in oak (*Quercus virginianus*) recruitment over time (Diefenbach et al. 2009). High herbivore densities have been observed to promote the survival of chemically or physically defended plant species, or of their less favoured resources, over other plant species. These changes ultimately alter plant–plant interactions, restructuring the entire plant community, both in terms of species composition (Riginos & Grace 2008, Ford et al. 2014, Atkins et al. 2019) and structure (Yovovich et al. 2021).

Conversely, one paper suggests that top-down regulation exerted by felids may also be detrimental to plant biomass and have negative cascading effects on vegetation regeneration when the limited species act as an important seed-disperser. Recent research experimentally demonstrated in Panama tropical forests where ocelot density was high that seed dispersal of a dominant palm species by agoutis was reduced, compared to study sites without ocelots, due to fear effects (Gálvez & Hernández 2022).

Beyond the effects discussed above, the loss of an apex felid species might trigger extensive trophic cascades with far-reaching effects on the entire ecosystem (LaBarge et al. 2022). Apart from indirect impacts on plant communities, several studies discussed associated ecological consequences such as changes on habitat structure (e.g. soil erosion, open water availability, canopy openness) and biodiversity integrity (e.g. Ripple & Beschta 2006, Terborgh et al. 2006, Lundgren et al. 2022). However, more robust investigations are required to substantiate these observations.

INTRAGUILD TROPHIC CASCADES

Initiated later than research on predator–prey interactions, a growing research effort is now focusing on the effects of intraguild interactions within ecosystems (Prugh & Sivy 2020). We identified 19 trophic cascades presumably initiated by interactions between felids and other carnivores, that appear to have indirect effects on other animal species and in one case, on a fruit tree species, dispersed by a frugivorous mesocarnivore (i.e. the red fox *Vulpes vulpes*). Reviewed studies provide arguments for the 'mesopredator release hypothesis' throughout the world, using mostly spatial, temporal or spatiotemporal approaches (Brashares et al. 2010, Harihar et al. 2011, Burgos et al. 2022).

Depending on the overlap between carnivore niches, the impact on prey communities can be detrimental. In most cases, prey species that were previously consumed by both the large carnivore and the released mesocarnivore, or exclusively by the latter, are reported to be severely affected by the expansion of the mesocarnivore population. By demonstrating efficiency in resource competition despite competition with larger species, mesocarnivores exhibit greater potential to exploit prey resources extensively compared to apex carnivores (Prugh et al. 2009). The outbreak of the opportunistic omnivorous olive baboon (*Papio anubis*), induced by the loss of lions and leopards in Ghana, provides a compelling example of the amplified effects caused by 'mesopredator release' (Brashares et al. 2010). This ecological shift has resulted in increased carnivorous dietary opportunities for baboons, leading to a significant decline in small primates and ungulates. On the contrary, the prey that was most exploited by the apex carnivore can increase, as demonstrated by other studies (Henke & Bryant 1999, Thinley et al. 2018). This change in prey abundance might also have negative cascading effects on general biodiversity integrity if the released prey is highly competitive or invasive within its guild (Paine 1969, Henke & Bryant 1999, Ritchie et al. 2012). We also found three studies documenting the benefits that the reintroduction or natural recolonisation of a felid apex carnivore in a landscape seem to have had on mesocarnivore prey (Palomares et al. 1995, Elmhagen et al. 2010, Jiménez et al. 2019).

Predicting the effects of an intraguild trophic cascade is particularly complex. Beyond aforementioned context-specific factors, it requires a thorough understanding of the system, including each carnivore's diet, predation efficiency, target prey demographics (i.e. juvenile vs. adult), and the density- and behaviourally mediated effects that these species-specific traits exert on prey (Ritchie et al. 2012, Haswell et al. 2017, Prugh & Sivy 2020).

By suppressing dominant mesocarnivores, apex carnivores can also have indirect positive effects on subordinate mesocarnivores, freeing some ecological niches and improving their fitness through scavenging opportunities (Allen et al. 2015, Newsome 2015). This phenomenon is known under the name of 'carnivore cascade hypothesis' (Levi & Wilmers 2012, Prugh & Sivy 2020). We found support for only seven trophic cascades among carnivores, in line with this hypothesis. Six studies involved the puma, in three different ecosystems of its range (Wang et al. 2020, Gil-Sánchez et al. 2021, Rodriguez Curras et al. 2022). For example, Allen et al. (2015) showed experimentally that pumas increase availability of carrion to small scavengers by limiting access to the mesocarnivore community. Others studies have confirmed that solitary felids play a critical role in redistributing energy flows by killing large prey (Monk & Schmitz 2022, Peziol et al. 2023). By facilitating nutrient distribution at their kill sites, they affect a highly diverse ecological community, providing mesocarnivores with expanded scavenging opportunities and access to additional dietary components (Elbroch et al. 2017, Barry et al. 2019, Barceló et al. 2022). These inhibitory and facilitative processes between apex and mesocarnivores are particularly complex to study (Prugh & Sivy 2020, Ruprecht et al. 2021). Yet, by promoting nutrient recycling and extensive food web linkages, felids are likely to have additional indirect effects on local ecosystem biodiversity, vegetation heterogeneity and productivity, but few studies have focused on these cascading effects so far (Teurlings et al. 2020, LaBarge et al. 2022).

Felids and trophic cascades in human-dominated landscapes

Twenty-two studies (36%) were carried out in protected areas characterised by minimal degradation and restricted access, or in regions featuring expansive natural habitats alongside low human population density [0–23 pers./km^2]. It is important to note that the North American systems categorised as 'well-preserved' have nonetheless experienced severe post-Pleistocene mammalian extinctions, resulting in an ecological simplification that sets them apart from other systems deemed relatively intact, such as some ecosystems in sub-Saharan Africa (Smith et al. 2022). On the other hand, 39 studies (64%) were conducted, at least partly, in degraded landscapes. These systems corresponded to protected areas severely disturbed by overhunting or tourism, or to habitats fragmented by human activities, such as expanding agriculture and urban development. In 44% of them, felids were no longer present due to their high vulnerability to direct (e.g. exploitation, persecution) and indirect (e.g. habitat loss, prey depletion) human pressures, and their role in trophic cascades was, therefore, studied by using control sites, time series or simulated cues of their presence.

Even in areas where felids have adapted to human presence through spatiotemporal avoidance (i.e. 'Landscape of Coexistence' concept; Oriol-Cotterill et al. 2015), disentangling the effects of wild cats on lower trophic levels from other confounding effects associated with human presence remains a challenge (Zanón Martínez et al. 2022). Factors such as hunting pressure on certain prey (top-down effect) or food subsidies provided by agricultural development (bottom-up effect) can alter the abundance of prey and mesopredator populations (Kuijper et al. 2016), making it difficult to precisely identify the actual or once fulfilled ecological role of felids in trophic cascades (e.g. Maina & Jackson 2003, Ickes et al. 2005).

Despite these difficulties, 14 studies aimed to investigate the implications of human presence on the ecological function of felids in food webs where they co-occur. They were categorised as 'human-induced trophic cascades'. Our findings are consistent with previous research suggesting that the role of large carnivores in trophic cascades is understudied in areas of high human-wildlife interface, and that existing studies primarily focused on felids living in suburban areas of the northern hemisphere (Kuijper et al. 2016, Elbroch et al. 2020). In most cases ($n=12$), our review revealed that the presence of humans inhibits the top-down effects of felid species on their prey (Muhly et al. 2011, Lendrum et al. 2018, Suraci et al. 2019) and competitors (Wang et al. 2015, Green et al. 2018, Zanón Martínez et al. 2022), notably by creating a 'human shield' against predation (Berger 2007), which in turn can lead to cascading ecological consequences (Ordiz et al. 2013, Yovovich et al. 2021). However, human activities could also exacerbate the predation pressure that felids exert on their prey or competitors. Gehr et al. (2018) observed that roe deer (*Capreolus capreolus*) were more susceptible to Eurasian lynx (*Lynx lynx*) predation when they sought refuge in forests during the hunting season, resulting in increased mortality in the population. Another notable example is the demonstrable trophic cascade triggered by pumas' fear of humans, which leads to reduced feeding time at their kill sites and a resulting compensatory increase in predation on deer (Smith et al. 2015, 2017).

These results are consistent with other studies indicating that the magnitude of carnivores' impacts in relatively undisturbed ecosystems is likely to differ from those observed in human-modified systems, often with human influence overshadowing carnivores' top-down control (Muhly et al. 2013, Kuijper et al. 2016, LaBarge et al. 2022).

RECOMMENDATIONS AND CONCLUSION

Our study provides a comprehensive synthesis of existing evidence supporting the claim that felids assume diverse and important ecological roles within their respective ecosystems. Some strongly inferential studies have confirmed that wild cats can have far-reaching effects on animal and plant communities through trophic cascades, particularly via behaviourally mediated effects. However, the main body of evidence is derived from non-experimental studies, that have not consistently accounted for potential confounders and explored alternative hypotheses, such as bottom-up processes. Therefore, we recommend further manipulative experiments under controlled and replicated conditions over sufficient spatial and temporal scales to identify causal factors. Robust correlative studies addressing underlying mechanisms and acknowledging their inability to assess causal relationships could support these experiments. We also encourage fostering collaborations between research institutions, universities, NGOs and local authorities to enable an interdisciplinarity approach and comprehensive studies, ensuring a more nuanced and non-distorted understanding of felids' contributions to ecosystem functioning.

Furthermore, this review undoubtedly reveals only a portion of felids' ecological functions, considering the lack of research on most small felids (<20 kg), and on wild cats in tropical and mountainous environments. Research focusing on mesocarnivores is particularly urgent for understanding the potential consequences of their projected ascension in food webs to adapt management and conservation strategies, and to preserve biodiversity, ecological processes, and intactness.

Our findings emphasise the limited number of publications on human impacts on felids' ecological functions within food webs. Such research is particularly needed as 1) human landscape dominance has, and broadly continues to increase in much of the globe, 2) felids naturally return or are reintroduced into modified environments, and 3) humans cannot adequately substitute the functional role of wild cats in ecosystems. While some ecosystem services provided by felids were identified in the reviewed studies (e.g. Brashares et al. 2010, Thinley et al. 2018), further quantitative assessments of these are urgently needed and should help to support their conservation on a global scale (e.g. Braczkowski et al. 2018, Puri et al. 2020).

By summarising the current understanding of felids' ecological roles and acknowledging their critical contributions to maintaining functioning ecosystems in specific contexts, we hope that this paper can enhance effective communication with key stakeholders. Translating the knowledge on felid trophic cascades into appropriate conservation policies and practices can further contribute to safeguarding these emblematic species and the ecosystems they inhabit. By highlighting the limited scope and variable quality of the evidence base for our understanding of felid-mediated trophic cascades, we aspire to encourage the growth and robustness of knowledge to inform on-the-ground conservation interventions.

ACKNOWLEDGEMENTS

We thank Robin Mosberg for graphic support. We also thank Matt W. Hayward, Peter M. Haswell, Ben L. Allen, Marius Ruwet, Simon Tossens, and an anonymous reviewer for their insightful comments and suggestions that improved the manuscript.

FUNDING INFORMATION

This work was supported by the Fund for Research Training in Industry and Agriculture (FRIA, F.R.S.—FNRS, grant [3] 47443), the ‘Programme de Promotion de l’Exploitation [4] Certifiée des Forêts’ (PPECF, grant C240), and Nature [5] plus ASBL.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

A full spreadsheet of the studies included in this review and their characteristics is available in the Supporting Information.

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SUPPORTING INFORMATION

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

Appendix S1. Decision tree used to define the environmental context (i.e. well-preserved vs degraded) of the study sites found in the literature review.

Appendix S2. Summary of studies included in this review and their characteristics (location, environmental context, methodological approach, assessment of alternative hypotheses, focal species, cascading impacts, and references).