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The Potential for Subordinate Predator Release in Terrestrial Mammalian Carnivore Assemblages

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ABSTRACT

1. Mesopredator release occurs when the decline of a dominant predator leads to an increase in a mid-sized predator due to reduced top-down pressure, often triggering cascading ecological effects. However, predator–predator interactions are complex and not strictly size-dependent.
2. We aimed to systematically review the evidence for suppressive relationships among terrestrial carnivores to assess the potential for subordinate predator release across different species and ecological contexts.
3. We conducted a systematic literature search up to February 2023, adapting previous frameworks. Studies were included if they demonstrated one carnivore suppressing another's population, which we used as a proxy for release potential. We categorised studies based on geographic location, species involved, methodology, and strength of evidence, ranking support from strength 1 (weakest) to strength 3 (strongest).
4. We found evidence for potential subordinate predator release across various size differences, challenging the traditional apex–mesopredator dichotomy. Inconsistencies in how authors perceived suppression highlight the need for caution in defining trophic roles in complex systems.
5. Canids and felids were equally represented as dominant carnivores in studies, but canids overwhelmingly occupied the subordinate role. This pattern may reflect their broader dietary niches and adaptability, but could also result from geographic research biases, particularly in the USA and Australia.
6. Our findings emphasise the need for more diverse, context-dependent studies to disentangle ecological mechanisms from research bias. Clarifying terminology and trophic classifications will enhance understanding of predator interactions and their ecological impacts.
7. Future research should focus on collating contradictory evidence to better understand the context dependency of intraguild interactions and analysing the strength of species responses to inform conservation and management strategies.

1 | Introduction

Mesopredator release is the ecological process that occurs when the local decline in the population of an apex predator causes the increase in the population of a subordinate mesopredator as a result of being released from top-down pressure (Prugh et al. 2009). Although the concept had been discussed in earlier literature, it was first defined by Soulé et al. (1988) in their work understanding how the absence of coyotes (*Canis latrans*) led to an increase in predation rates on chaparral bird species by red foxes (*Vulpes vulpes*), house cats (*Felis silvestris catus*) and other mesopredators. This process has been theorised to be more likely between two species with overlapping trophic niches and therefore more likely between species with intermediate body size differences, for example, between 10% and 30% (Woodward and Hildrew 2002; Van Schaik et al. 2024). However, some studies have shown that mesopredator release can occur more often in species with larger (> 30%) size differences, especially within European systems (Van Schaik et al. 2024).

The release process could occur due to dominant species' suppression of a subordinate species at different trophic levels independent of their size differences. One example is between grey wolves (*Canis lupus*) behaving as the dominant species and larger mountain lions (*Puma concolor*) as the subordinate species (Elbroch et al. 2020), neither of which could be considered mesopredators. A more traditional example is the big-eared opossum (*Didelphis aurita*), a mesopredator that limits the population sizes of the smaller brown four-eyed opossum (*Metachirus nudicaudatus*) (Kuhnen et al. 2019). Here we opted to use the broader term 'subordinate predator release' (Swanson et al. 2016) which, although not commonly used, is more encompassing of the variety of trophic levels this process can impact. We interpret this as distinct from competitor release, even though competitor release has been used in studies which show one species having dominance over another. For example, Caut et al. (2007) refers to 'superior' and 'inferior' competitors and Azevedo et al. (2012) refer to a 'stronger' and 'weaker' competitor. These two examples would be indicative of subordinate predator release, competitor release would more appropriately describe a relationship between two equal competitors, where both species are supressed by the presence of the other and either could experience release if the other declined.

With the numerical decline of a dominant predator and subsequent increase of a subordinate predator, subordinate predator release disrupts the balance of predator–prey interactions, leading to cascading effects on lower trophic levels and altering community structure (Ritchie and Johnson 2009). The ecological significance of subordinate predator release extends its influence on prey populations, plant communities and ecosystem processes, with observed consequences for biodiversity and ecosystem stability (Prugh et al. 2009; Levi and Wilmers 2012; Russell et al. 2009; Brashares et al. 2010). Understanding the global occurrence of this process can help predict ecological outcomes in regions where predator dynamics are shifting and provide insights into how predator–prey dynamics vary across different regions and ecological contexts.

In terms of conservation, poor understanding of the occurrence of subordinate predator release poses challenges for managing threatened or endangered species, preserving trophic cascades and maintaining ecosystem resilience. On one hand, if it occurs unexpectedly, then conservationists may not have plans in place to mitigate its cascading effects. On the other hand, if conservationists assume that subordinate predator release is going to happen when a dominant species declines, it could lead to a misunderstanding of the species risk of extinction. Furthermore, the complexity of ecological interactions and the unpredictability of ecosystem responses present research and management challenges. With rapidly changing ecosystems through processes such as habitat degradation and, on the other side, rewilding and reintroductions, it is essential that we understand the processes that regulate predator populations and their subsequent ecosystem-level impacts. Another complexity in identifying subordinate predator release is distinguishing it from competitor release. Accurately distinguishing between the two would require either controlled experimental study areas or a very specific set of comparable scenarios which are unlikely to occur in practice.

A systematic review of the literature on mesopredator release from North America was conducted by Jachowski et al. (2020) who found that there is strong but inconsistent evidence for mesopredator release in certain species assemblages. They also found that 64% of studies were showing correlation rather than causation and questioned whether short-term changes in mesopredator populations due to a reduction in top-down pressures will always persist in the long term. This lack of consistent evidence is compounded by the fact that a large proportion of the publications showing the process come from studies focused on canids, in particular grey wolves (Saggiomo et al. 2021), introducing bias. A literature trend analysis on mesopredator release by Saggiomo et al. (2021) showed that the only felid species in the top 20 most common keywords was the domestic cat *Felis catus* (Saggiomo et al. 2021). Similarly, Jachowski et al. (2020) found that only 23% of studies in North America studied felid species as either the apex or subordinate predator. Felids are highly specialised in terms of feeding ecology and habitat use, which may make it difficult for them to display behavioural plasticity and persist in new environments (Teixeira et al. 2020; Raia et al. 2016). Canid species are often generalists, so they may have a higher adaptability than felids, which are often specialised, to the threats that cause the local extinction of large carnivores (Prugh et al. 2009; Dotta and Verdade 2007; Yusefi et al. 2021). This could mean that subordinate felids are less likely to experience release and may instead decline as a result of the same threats as dominant species, whilst subordinate canids are able to persevere and even thrive.

Importantly, not all evidence is equal when it comes to showing subordinate predator release. To that end, Jachowski et al. (2020) developed a conceptual framework that offers guidelines on how to evaluate the strength of evidence provided by a study for the occurrence of mesopredator release. This framework considers the scale at which a response is recorded, considering the study's spatial, temporal and ecological scope. For instance, they argue that a study documenting space use at an individual level is less robust evidence than one showing changes in community distribution over time. Under their framework, 'release' is determined when a study shows changes in a population's abundance over time. van Schaik et al. (2024) have since applied Jachowski et al. (2020) methodology to a European context to understand how mesopredators respond to both the decline and increase of apex predators.

In this review, we aim to apply a simplified version of the framework developed by Jachowski et al. (2020) to assess the methodological strength of the evidence for subordinate predator release in different carnivore species pairings on a global scale. Herein, when referring to carnivores, we mean mammals, including marsupials, whose diet is primarily carnivorous. We focus on studies showing demographic-level effects, such as abundance and occupancy, not behavioural effects, such as activity patterns or dietary shifts. By encompassing a broader range of habitats and environmental conditions, this systematic review can provide a comprehensive overview of subordinate predator release phenomena, highlighting patterns and research efforts across different regions and guiding future research directions in this field.

2 | Methods

2.1 | Search Strategy

We conducted a systematic search for peer-reviewed publications on Scopus (www.scopus.com), Google Scholar (www.scholar.google.com) and three Web of Science databases; Core Collection, BIOSIS Citation Index and Zoological Record (webofscience.com) to collate the literature on subordinate predator release in carnivores from terrestrial systems around the world. We included all publications up to February 2023. On Web of Science databases, we limited the search to 'Topic' and Scopus we searched 'Article title, Abstract, Keywords'.

We used a search string composed of two components:

2.1.1 | Genera of Species

This section includes the list of genera of carnivores that were used as search terms to identify relevant studies on mammalian mesopredator release. We initially conducted a search for each carnivore genus separately (with the full second component) before combining all genera that produced results to generate the final search string.

2.1.2 | Ecological Terms

This section comprises the keywords and phrases related to the ecological process of interest (competition, interspecific interaction, intraguild, interguild, trophic cascade, mesocarnivore release, mesopredator release and competitor release). These terms were used to identify studies focusing on the dynamics of mammalian mesopredator release from terrestrial systems around the world. This step collated papers that showed the potential for subordinate predator release even if it was not interpreted by the authors as such.

The full string (Appendix S1) was used in both the Scopus and Web of Science searches. However, to adhere to the maximum character count for Google Scholar ($N = 256$) the string was split into 12 separate strings with six genera per search. The full results from both Scopus and Web of Science were extracted for review, and the first 10 pages of results (ordered by relevance), after which results became irrelevant, per search in Google Scholar were exported and reviewed for inclusion. Deduplication between the results from the different databases was conducted in Endnote 20.4.1 using their auto deduplication tool and then manual screening. The remaining results were then screened in two stages structured similarly to Jachowski et al. (2020); the first was a review of titles and abstracts and the second was a review of full text (Figure 1). Articles proceeded to stage two if the title and abstract referred to terrestrial mammals and included the simultaneous monitoring of the abundance or distribution of two or more carnivores from primary data. If it was unclear, then the article would also be reviewed at the second stage (full text). The

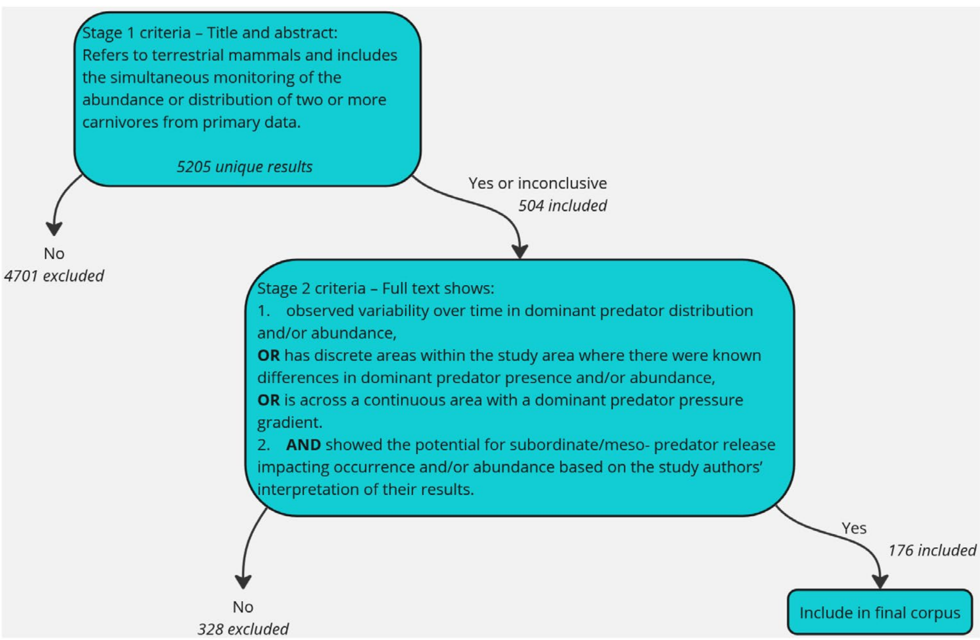

FIGURE 1 | Flow chart showing the process of inclusion in the systematic review on the potential for subordinate predator release between carnivores through two different stages.

second stage identified papers where results indicated suppression of one carnivore on another's population as a proxy for the potential for subordinate release based on the study authors' interpretation of their results. To be included at this stage, the study needed to meet two criteria (Figure 1): studies had to (1) be conducted over time, across discrete areas or across a continuous area with a recorded gradient of dominant carnivore presence, and (2) show the potential for subordinate predator release. Articles were excluded if they showed mutual avoidance, if it was unclear who avoided whom, or if the methods were unclear. Only publications that had gone through peer review were included. All articles that met the second set of criteria were included in the final analysis. All reviewing was done manually.

2.2 | Search Validation

A second reviewer evaluated 5% ($N=260$) of the search results using the same criteria, and we then conducted a Kappa analysis to assess inter-reviewer agreement. The analysis indicated 'substantial agreement' ($\kappa=0.63$), confirming consistency in the study selection process.

2.3 | Bias Assessment

In considering the potential biases within our systematic review methodology, several factors were taken into account. We decided not to include any grey literature for this systematic review to maintain a focus on peer-reviewed publications, which typically undergo rigorous quality control processes. However, this decision may have introduced a potential source of bias by excluding valuable insights from sources such as conference abstracts or unpublished studies. Only papers translated into English were included, which may have excluded relevant studies published in other languages and led to language bias and geographical bias. However, this decision was made to ensure consistency and accessibility of the literature for analysis. The impact of publication bias (e.g., only studies with positive results being published) is limited in this search, as we were specifically only interested in articles with results demonstrating the potential for subordinate predator release, and collating those that did not show such potential was outside the scope. Taxonomic bias is another consideration, as predator species not included could also exhibit subordinate predator release, but this was beyond the scope of our study. Despite the systematic approach to screening articles, there is still the potential for selection bias during the screening process. Human reviewers may inadvertently bias the selection of articles based on their own judgements or interpretations of relevance criteria, but this is mitigated through the kappa analysis. Additionally, as the final corpus was reviewed by the lead author, any impact of selection bias during the final stage was consistent.

2.4 | Data Extraction and Synthesis

We retrieved the following information from the full text from each article: year of publication, authors, title, country of study (e.g., United States), location of study (e.g., Olympic National Park), dominant species Latin name, subordinate species Latin name, method of data collection, method of analysis and study design details (e.g., over time or space-for-time). If a study analysed the interaction between multiple pairs of species, then an entry was included for each individual pair that showed subordinate predator release. This data was then joined with the taxonomic information for each species in the pair using taxonomic information from the American Society of Mammalogists (2024) and size information from Myers et al. (2006). The size data was then used to group the species into three different size categories: small (< 5 kg), medium (5–20 kg), and large (> 20 kg) (Carbone et al. 2007). We then conducted descriptive comparisons of the data, examining three aspects of the articles: (1) the geographic location of the studies, (2) the species involved and (3) the methods used. Analysis was conducted in R (R Core Team 2022) and figures were generated using ggplot2 (Wickham 2016).

2.5 | Methodological Strength of Support

To assess the methodological strength in a paper for supporting the potential occurrence of subordinate predator release between their study species, we built off Jachowski et al. (2020)'s framework and focused on two key considerations:

a. Space-for-time or over time: This compares studies that use spatial patterns to infer a relationship between dominant and subordinate populations versus those that directly track changes in populations over time.
b. Space use (how individuals use resources within their ecosystem) or abundance or distribution: This evaluates whether studies focus on how species use space, their population abundance or their spatial distribution. If a paper assessed both space use and abundance, then it was categorised as abundance.

We then used these considerations to categorise the reviewed papers into three groups (Figure 2):

1. Strength 1: These studies indicate there might be a connection between dominant and subordinate predator populations and therefore they have the potential to exhibit subordinate predator release. However, the evidence is not strong enough yet and requires more thorough investigation. Papers which used space-for-time and analysed individuals' space-use were put into this category.
2. Strength 2: These studies offer strong enough evidence that it is reasonable to think that the dominant species is suppressing the subordinate species population, but it is not yet definitively proven. This category was applied to papers which used space-for-time and analysed either species abundance or distribution or papers which studied species space-use over time.
3. Strength 3: These studies provide compelling evidence that the connection between the two species is highly likely, and the release of the subordinate predator, if the

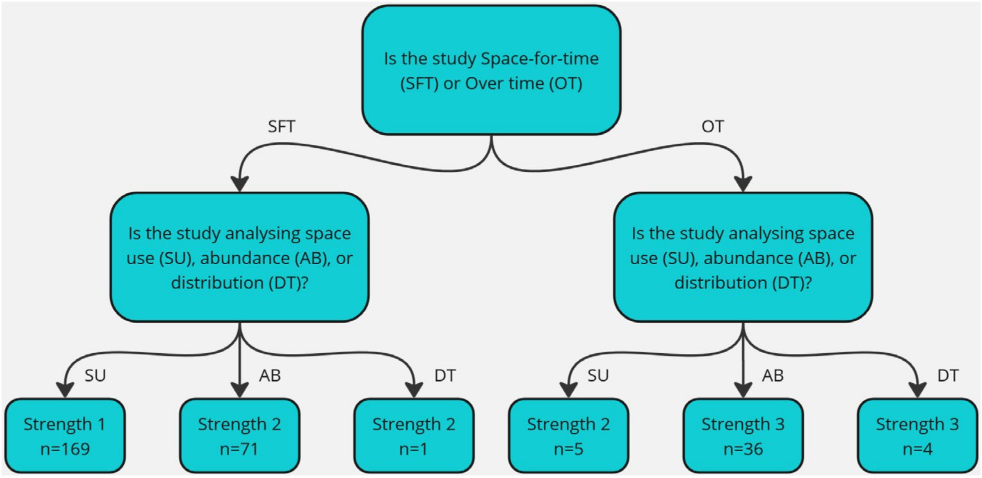

FIGURE 2 | Flow diagram of the scaling of methodology strength used for showing the potential for subordinate predator release process for the papers including the number that ended up in each category. AB, Abundance; DT, Distribution.OT, Over-time; SFT, Space-for-time; SU, Space-use.

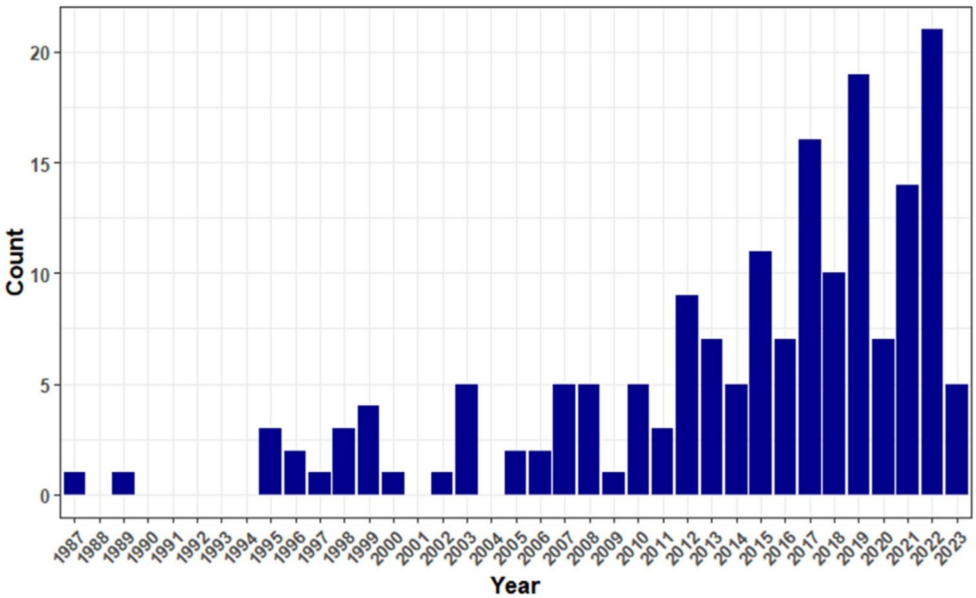

FIGURE 3 | Counts of papers which met our search criteria for showing the potential for subordinate predator release between two carnivore species per year from 1987 to 2023.

dominant predator is reduced, is very likely to occur given the right conditions. If a paper studied species changes in abundance or distribution over time, then it was categorised into this group.

3 | Results

We conducted the initial search on 8th February 2023 with Web of Science and Scopus yielding 3878 and 2541 results, respectively. A subsequent search on Google Scholar on 28th November 2023, which was limited to the same time frame as the previous searches, yielded an additional 1051 results. After eliminating duplicates, we identified 5205 unique records. Of these, 504 met Criteria 1 and had accessible full texts, whilst 176 met Criteria 2 and were subsequently included in our systematic review (Figure 1). Although the earliest article dates to 1987 (Figure 3), the onset of consistent publications began in 1995, with three articles published that year. The publication rate remained relatively steady until 2012, when it reached 26 articles. Prior to 2012 (not including 2023 as it was not a full year) the average annual publication rate was 1.80 ± 1.79; since 2012, it has been 11.45 ± 5.09 articles.

These articles collectively represented studies conducted across 38 countries spanning six continents (Figure 4, Appendix S2 Table S2.1). North America contributed 67 papers (38.1%), followed by Africa with 31 (17.6%), Europe with 25 (14.2%), Asia with 21 (11.9%), Oceania with 21 (11.9%) and South America with 13 (7.4%). The first publication was in 1996 for both South America and Africa, 2005 for Asia, and 2009 for Oceania. Since 2012, the proportions of pair studies per continent have fluctuated yearly (Appendix S2 Figure S2.1). For each continent, the country with the highest number of pair studies

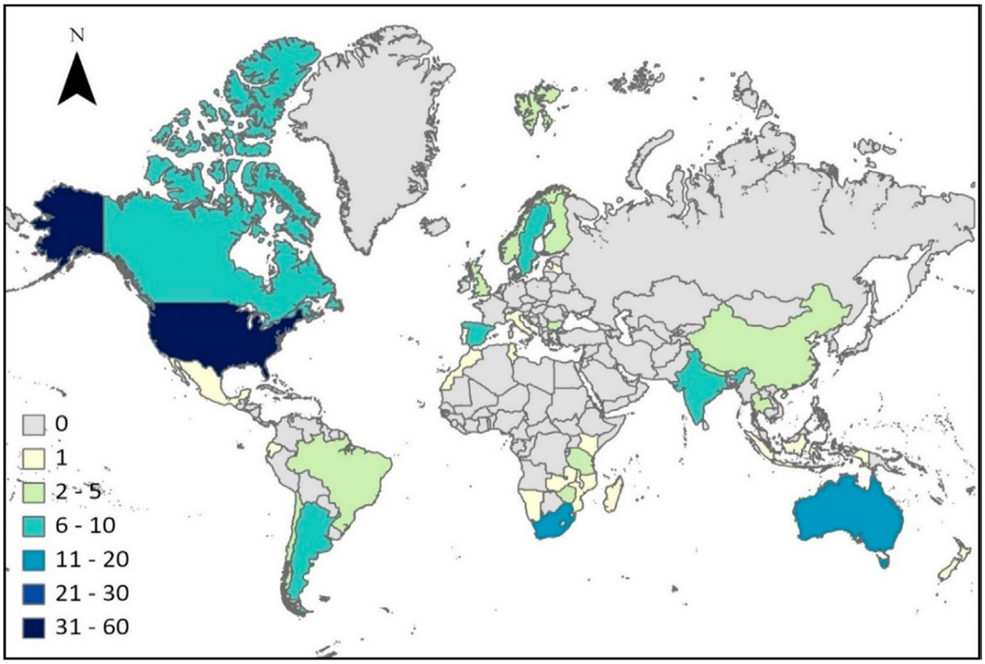

FIGURE 4 | Map showing the number of papers which met our search criteria for showing the potential for subordinate predator release per country.

was as follows: North America: USA (n = 60, 89.5%), Africa: South Africa (14, 45.2%), Europe: Spain (6, 24.0%), Asia: India (7, 33.3%), Oceania: Australia (20, 95.2%) and South America: Argentina (6, 46.2%).

3.1 | Methodological Strength of Support

Forty of 176 studies (22.7%) were conducted over time compared to 136 (77.3%) that used a space-for-time approach. One hundred and one (54.5%) studies analysed the space use of individuals within their ecosystem, 76 (43.2%) analysed the abundance, whilst four (2.3%) analysed the distribution. This resulted in 91 papers (51.1%) providing strength 1 evidence of at least one species pair having the potential for subordinate predator release, 50 (28.4%) showing strength 2 evidence, and 35 (19.9%) showing strength 3 evidence. There were 17 different types of data used in the studies, with camera traps being the most frequent, being used in 78 studies (44.6%) and dominating since 2011, followed by telemetry data with 27 (15.3%) and track surveys with 21 (11.9%) (Appendix S3 Table S3.1 and Figure S3.1). Fifty different categories of statistical analysis were used to study species pairs, the most common of which was occupancy modelling, used in 48 studies (26.7%), followed by abundance indices with 40 (22.7%) (Appendix S3 Table S3.2 and Figure S3.2).

3.2 | Taxonomic Classification of the Studied Carnivores

From the 176 included papers, there was a total of 286 species interactions recorded exhibiting subordinate predator release, with a maximum of 15 pairs in one paper (Curveira-Santos et al. 2021), resulting in 161 unique pairs studied. The dominant species spanned nine different taxonomic families, whilst the subordinate species spanned 12. Canidae was the most frequent dominant species, with 127 pairs (44.4%), closely followed by Felidae with 126 (44.1%). Additionally, Canidae were identified as the subordinate species in 134 pairs (46.9%), whilst Felidae had 73 pairs (25.5%). Other taxonomic families had fewer mentions in the literature, with an average of 4.71 ± 3.15 per family for non-Canidae and non-Felidae dominant species (totalling 11.5%) and 7.90 ± 7.37 for subordinate species (23.6%).

In total, we identified 45 different dominant species, with coyote (*Canis latrans*) being the most frequent, documented in 42 pairs (Appendix S4 Table S4.1). African lion (*Panthera leo*) followed closely with 36 pairs and grey wolf (*Canis lupus*) with 24. Our analysis revealed 86 different subordinate species, with red fox (*Vulpes vulpes*) being the most frequently studied, appearing in 46 pairs. This was followed by grey fox (*Urocyon cinereoargenteus*) with 15 pairs and coyote with 14. From the 286 pairs we identified, there were 164 unique species pairs, which consisted of 32 unique family pair combinations. There were 142 pairs involving species from two different families, with 86 being exclusively Canidae species and 48 being exclusively Felidae species (Figure 5). A total of 18 pairs were identified as Canidae—Felidae (dominant—subordinate) whilst 42 were Felidae—Canidae. The most frequently observed species pairs were *Panthera leo—Lycaon pictus* and *Canis lupus dingo—Vulpes vulpes*, each documented in 11 articles, followed by *Canis latrans—Vulpes vulpes* and *Canis lupus—Canis latrans*, each in 10 articles (Table 1).

When considering the total number of instances across studies, there were 169 pairs of species with strength 1 support (59.1%), 77 with strength 2 support (26.9%), and 40 with strength 3 support (14%) (Figure 2). When focusing on unique species pairs

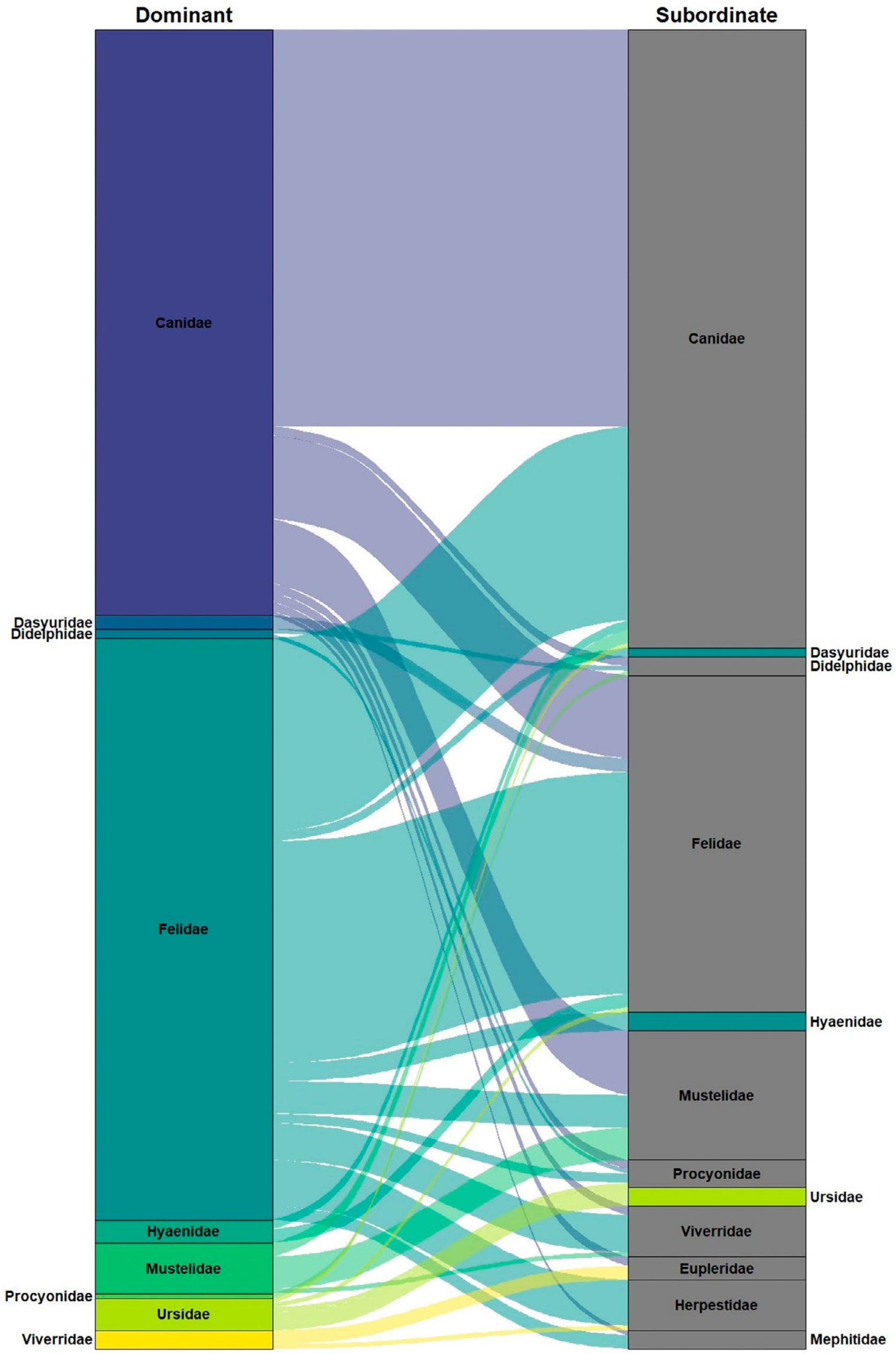

FIGURE 5 | Frequency of different species taxonomic family's combinations with dominant species family on the left and subordinate species family on the right, the width of the ribbons connecting the two are proportional to the number of papers studying a pair of that family combination. The colour of the subordinate family is grey if it is impacted by multiple families of dominant, but coloured if it is only impacted by one family.

classified by their highest level of support, there were 89 pairs with strength 1 support (55.3%), 47 with strength 2 support (29.2%), and 25 with strength 3 support (15.5%) (Table S5.1). Eight of the top 10 most studied pairs had the highest level of support, strength 3, for the potential for subordinate predator release, while the remaining two still had strong support with strength 2 evidence. Only two pairs, which only had one study, reached the threshold to show strength 3 evidence: *Canis lupus* (Grey wolf)—*Lynx canadensis* (Canada lynx) and *Didelphis aurita* (Big-eared opossum)—*Metachirus nudicaudatus* (brown four-eyed opossum) (Appendix S5 Table S5.1).

The most common size for both subordinate and dominant species was medium, occurring 140 times as the subordinate species (49.0%) and 145 as the dominant (50.7%) (Appendix S6 Table S6.1). The most common size pair was medium–medium

TABLE 1 | All pairs studied more than once, and the highest strength of support shown (strength 1 < strength 2 < strength 3) for the potential of subordinate predator release based on their methodology. The full table can be found in Appendix S5 Table S5.1.

Species pair	Count of studies	Strength of support	Species pair	Count of studies	Strength of support
Canis lupus dingo—Vulpes vulpes	11	Strength 3	*Sarcophilus harrisii—Felis catus*	3	Strength 3
Panthera leo—Lycaon pictus	11	Strength 3	*Vulpes vulpes—Martes martes*	3	Strength 3
Canis latrans—Vulpes vulpes	10	Strength 3	*Vulpes vulpes—Vulpes lagopus*	3	Strength 3
Canis lupus—Canis latrans	10	Strength 3	*Canis latrans—Martes americana*	2	Strength 2
Canis latrans—Urocyon cinereoargenteus	8	Strength 2	*Canis lupus—Lynx lynx*	2	Strength 3
Panthera tigris—Panthera pardus	8	Strength 3	*Crocuta crocuta—Lycaon pictus*	2	Strength 2
Canis latrans—Vulpes macrotis	7	Strength 3	*Cuon alpinus—Vulpes vulpes*	2	Strength 2
Canis aureus—Vulpes vulpes	5	Strength 3	*Leopardus pardalis—Leopardus tigrinus*	2	Strength 2
Lynx pardinus—Vulpes vulpes	5	Strength 3	*Lupulella mesomelas—Vulpes chama*	2	Strength 2
Pekania pennanti—Martes americana	5	Strength 2	*Lynx pardinus—Genetta genetta*	2	Strength 1
Canis latrans—Lynx rufus	4	Strength 1	*Lynx pardinus—Martes foina*	2	Strength 1
Canis lupus—Vulpes vulpes	4	Strength 3	*Lynx rufus—Urocyon cinereoargenteus*	2	Strength 1
Lynx lynx—Vulpes vulpes	4	Strength 3	*Lynx rufus—Vulpes vulpes*	2	Strength 1
Lynx pardinus—Herpestes ichneumon	4	Strength 3	*Panthera leo—Crocuta crocuta*	2	Strength 3
Lynx rufus—Lynx canadensis	4	Strength 3	*Panthera onca—Puma concolor*	2	Strength 2
Panthera leo—Acinonyx jubatus	4	Strength 2	*Panthera pardus—Acinonyx jubatus*	2	Strength 2
Panthera leo—Panthera pardus	4	Strength 2	*Panthera tigris—Canis lupus*	2	Strength 3
Canis latrans—Vulpes velox	3	Strength 2	*Puma concolor—Canis latrans*	2	Strength 1
Canis lupus—Canis aureus	3	Strength 3	*Puma concolor—Lycalopex culpaeus*	2	Strength 1
Canis lupus dingo—Felis catus	3	Strength 2	*Vulpes vulpes—Neogale vison*	2	Strength 3
Lycalopex culpaeus—Lycalopex grises	3	Strength 3	*Vulpes vulpes—Urocyon cinereoargenteus*	2	Strength 1
Panthera tigris—Cuon alpinus	3	Strength 2	*Vulpes vulpes—Vulpes macrotis*	2	Strength 1

occurring 80 times (28.0%) (Figure 6, Appendix S6 Table S6.2). There were 142 interactions (49.7%) that documented species within the same size categories whilst three (1%) were recorded with the dominant species from a smaller size category. The total number of pairs where the dominant species was a larger size category than the subordinate species was 141 (49.3%).

Large-medium and large-large species pairings had the highest proportion of the two strongest evidence categories (strength 2: 29%–50.9% and strength 3: 24%–51.1%, respectively) (Figure 7). None of the studies focused on large-small species pairings provided 'strength 3' evidence. For all size pairings, the highest proportion of studies provided only 'strength 1' evidence (171%–59.8%).

4 | Discussion

4.1 | Evidence of Subordinate Predator Release and Research Implications

Our results show an equal representation of canids and felids as dominant carnivores within the literature showing the potential for subordinate predator release, but a predominance of canids in the subordinate position. This pattern may indicate either an ecological tendency for subordinate canids to have a higher potential to experience release or a bias in research focus towards canid species. It may be that canids are more commonly limited by top-down pressure; however, this seems contradictory to their dietary generalisation (Fleming et al. 2017). This broad dietary breadth may mean that they are more readily able to take advantage of the decline in large carnivores than many felids, which are commonly dietary specialists (Brashares et al. 2010). Additionally, the social system of canids is unique among carnivores because it is based on monogamy and biparental care of young (Macdonald et al. 2019) which supports higher social intelligence and larger group sizes compared to felids and other carnivore families (Macdonald et al. 2019). Whilst these facts may make canids more likely to be dominant over other families or to experience release if suppressed, these facts may also make canids more adaptable to competitive interactions, and so we would expect them to be less frequently suppressed than other families.

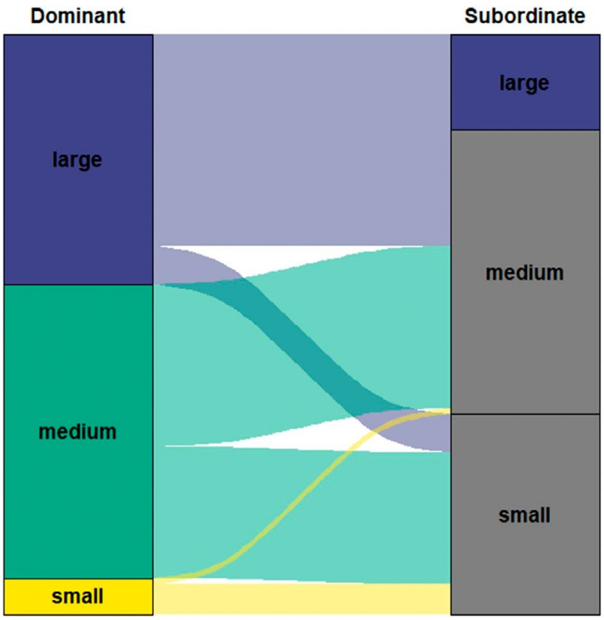

FIGURE 6 | Alluvial plot of the size category between carnivore pairs with dominant species size on the left and subordinate species on the right. The width of the ribbon indicates the number of studies on a pairing of that combination which showed the potential for subordinate predator release.

Brooke et al. (2014) also found Canidae to be the most studied species of carnivore overall. However, in contrast to our study, when calculating the mean number of papers per species in a family, they found that Ursidae had the most papers. Even when accounting for the number of papers per species, we still found that Canidae was the most common, and in the cases where studies did include a bear, it was usually interacting with another bear species (e.g., Ji et al. 2022; Apps et al. 2006). This lack of ursids in subordinate predator release studies, despite them being one of the most commonly studied carnivores more generally, could be indicative of them having minimal negative top-down effects on other species due to their more omnivorous diets (Bojarska and Selva 2012; Robbins et al. 2004) and large size difference with the majority of other carnivores (Hilderbrand et al. 2018; Brooke et al. 2014; Gittleman 1985). It is possible that bears may have a more facultative influence on other carnivores through the provisioning of carrion, although this seems to be context and species dependent (Allen et al. 2015; Prugh and Sivy 2020). There is also the chance that rather than being purely ecologically related, this could in fact reflect a bias in research on bears in isolation rather

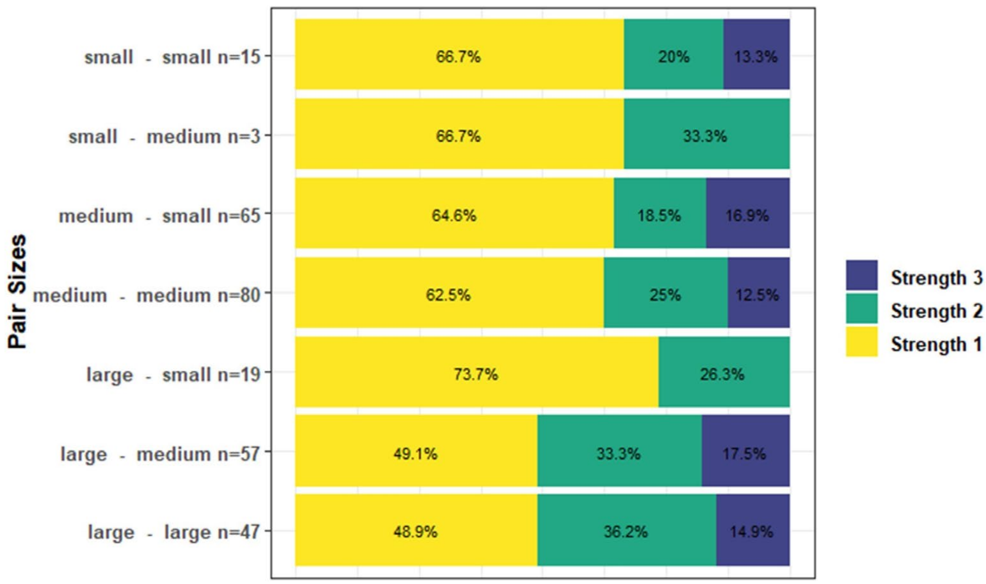

FIGURE 7 | Proportions of each size pairing that were categorised into the three different strength of evidence categories for the potential for subordinate predator release.

than as part of the wider carnivore community due to their significant size difference in many ecosystems.

Whilst positions in interactions were not identified, previous research has identified a taxonomic bias within the research on subordinate predator release, with canid species, notably grey wolves, dominating the literature (Saggiomo et al. 2021), providing an alternative explanation for the observed pattern. Canids such as wolves (Mech 2017), coyotes (Poessel et al. 2017) and jackals (Nattrass et al. 2020) are regularly reported as coming into conflict with humans, which could lead to a bias in research attention. Another possible cause of the dominance of canids could be a result of the geographical bias in research on intraguild interactions and cascading effects to the USA and Australia, where canids have broader distributions and higher population densities than most other carnivores (Laliberte and Ripple 2004; Glen and Dickman 2014). These study systems also do not have as high carnivore species diversity compared to systems such as East African savannahs (Dalerum et al. 2009), and so this bias could be due to the difficulties in disentangling the relationship in more complex systems. In more diverse systems, showing the limiting effect of one species on another becomes more complex and, as discussed by van Schaik et al. (2024), not studying a community in its entirety may lead to improper interpretations of interspecific relationships. Determining if the predominance of canids in subordinate predator release dynamics stems from ecological processes or research bias requires further investigation.

Subordinate predator release may vary between pairs that exhibit this phenomenon in one system but not in another, as it is context-dependent (Jachowski et al. 2020). Resource availability is a key influencing factor (Brashares et al. 2010; Van Schaik et al. 2024; Prugh et al. 2009), and Elmhagen and Rushton (2007) demonstrated that landscape productivity directly mediates this release. Crucially, resource availability is affected by anthropogenic impacts, climatic stressors and interspecific competition. An extreme example of how important the local context is would be the lion and African wild dog (*Lycaon pictus*) which was the most studied pairing. We found strong evidence that African wild dogs would exhibit subordinate predator release with the decline of lions (e.g., Mills and Gorman 1997; Strampelli et al. 2023; Swanson et al. 2014; Darnell et al. 2014). However, this relationship will be context-dependent and based upon the cause of the decline of lions because wild dogs would be equally, if not more, vulnerable to many human pressures that would cause lion population declines (Creel and Creel 1998). Another example would be our finding that it is possible that a decline in bobcats would cause an increase in lynx populations (e.g., Peers et al. 2013; Scully et al. 2018; King et al. 2021). However, unless human persecution targets bobcats but not lynx, it is unlikely that bobcat populations would decline relative to lynx. We emphasise that our categorisations of the strength of support in papers that found the potential for subordinate predator release should not be taken as evidence that it will occur in all systems where that pairing is found. For our lower and middle categories, we strongly advise that more research is needed to understand the dynamics between the two species in specific locations.

4.2 | Implementation of Jachowski et al. (2020)

Whilst we were using the broad framework created by Jachowski et al. (2020), our methods did differ in certain ways. The first was the inclusion of studies with continuous study areas using a space-for-time approach in addition to those with discrete areas in our search protocol. We acknowledge that occurrence patterns within a continuous survey area can be highly correlated to ecological factors aside from conspecific interactions. However, we believe there is value in including studies across a continuous area, as long as they have a demonstrable gradient of dominant carnivore occurrence, given that the study would have been included if the two opposing areas of the gradient had been studied as discrete areas. Whilst it is possible for the results of such studies across continuous areas to be impacted by unmodelled habitat differences (Gehrt and Clark 2003), this can also be the case for discrete areas. Acknowledging the potential for ambiguity with these surveys, we have ranked the strength of evidence they provide in comparison to surveys across discrete areas or over time, accordingly. We also chose not to include studies on pure behavioural aspects of interactions between carnivores, such as dietary, predation, or temporal studies, but instead focused on studies that were measuring some type of population metric. Whilst behavioural changes such as dietary shifts or changes in activity patterns may be a precursor to spatial exclusion (Haswell et al. 2020), this is weaker evidence than recorded differences in occurrence or abundance and so would be categorised as lower than our three groupings.

Jachowski et al. (2020) only included studies which monitored 'clear trophic order differentiation,' and Van Schaik et al. (2024) included studies where 'at least one must occupy a higher trophic order.' We did not specifically state this in our inclusion criteria as discerning what trophic level a species is can be difficult in some of the more complicated carnivore communities such as sub-Saharan Africa where there can be 15 sympatric species of carnivores over 5 kg. There were three cases where a study was interpreted as showing a small species supressing a medium species. Two of these were: margay and bobcat in Mexico (Sánchez-Cordero et al. 2008) and Virginia opossum and raccoon in Ohio, USA (Rich et al. 2018). Both studies were classed by our scoring process as providing 'strength 1' evidence. However, given the ecology of these pairs and other research showing the opposite direction of suppression identified in this review, this suppression seems unlikely (Ginger et al. 2003; Harmsen et al. 2021). This highlights the potential inaccuracies of differentiating trophic orders and distinguishing between subordinate predator release and competitor release. Additionally, trophic level overlap can be highly context-dependent and linked to resource availability (Périquet et al. 2015), human pressures and activity patterns (Gaynor et al. 2018) and community complexity (Thompson et al. 2007). By predefining trophic levels and differentiation criteria, we risked excluding relevant studies that contributed valuable insights into subordinate predator release dynamics across varying ecological contexts.

Contrary to the findings of van Schaik et al. (2024) in Europe, our global analysis shows the weakest evidence for release between large and small species (Figure 7). This may be due to the differences in carnivore dynamics influenced by habitat, prey availability and human activities in Europe (Haswell et al. 2017), or from methodological differences, even though both frameworks were based on Jachowski et al. (2020). Our inclusion criteria were broader than Van Schaik et al. (2024) which, whilst allowing for a more comprehensive analysis, may have introduced a wider range of study quality. Whilst our filtering process did not exclude papers such as Sánchez-Cordero et al. (2008) and Rich et al. (2018), where the recorded direction of suppression seems ecologically questionable, we do note that overall, only one pair in the top 30 most-studied pairs scored the weakest level of evidence. This indicates that our scoring system effectively differentiated most studies based on quality and robustness, underscoring the need for more research on many of the pairs studied less frequently.

4.3 | Subordinate Predator Release Over Mesopredator Release

We found multiple studies indicating potential 'release' effects within trophic levels. For instance, several studies analysed how Eurasian lynx limit red fox populations across various ecosystems, where both are typically considered mesopredators. Similarly, interactions between fishers and American martens illustrate mesopredator—mesopredator suppression. We also found studies showing coyotes impacting red foxes in systems both with and without wolves, complicating their classification as mesopredators or tertiary predators.

There were 19 large-small species pairs (11.9%) identified in the review, deviating from the traditional assumptions of suppression linking to body size. Fourteen of these pairs were categorised as strength 1 and 5 as strength 2. In all cases, the dominant species belonged to the Felidae family, including African lion (nine pairs), mountain lion (five pairs), tiger (*Panthera tigris*, three pairs), and leopard (*Panthera pardus*, two pairs). These species suppressed a range of subordinate species across families: five Viverridae, four Herpestidae, four Felidae, three Canidae, two Mephitidae and one Mustelidae. The strength 2 pairs were *Puma concolor* (mountain lion)—*Leopardus tigrinus* (oncilla), *Puma concolor* (puma)—*Leopardus wiedii* (margay), *Puma concolor* (mountain lion)—*Lycalopex griseus* (South American grey fox), *Puma concolor* (mountain lion)—*Mephitis mephitis* (striped skunk), and *Panthera tigris* (tiger) and *Vulpes bengalensis* (Bengal fox). The prevalence of Felidae in these pairings could indicate that large cat species can have a wider suppressive effect than large species of other families. This may be because large felids have greater niche overlap with smaller carnivores due to similarities in hunting strategies and diets, compared to other large species like canids (Piña-Covarrubias et al. 2023; Tossens et al. 2025).

A more extreme example that does not conform to traditional body size differences involves the fisher and grey fox in Oregon, USA (Green et al. 2018), which was the third pairing showing a small species limiting a medium species. This study provided strength 2 evidence that the smaller fisher was limiting the population of the larger grey fox in a system with larger carnivores present. Given the bias in research towards large carnivores (Tensen 2018; Brooke et al. 2014), it seems likely that more of these untraditional pairs, as well as more medium–small pairs, would be discovered if there were an increase in the proportion of research on smaller carnivores. These examples, in addition to the suppression seen in pairs where both could be considered apex predators (e.g., tiger and leopard), highlight the inherent ambiguity of splitting species into trophic levels in complex systems (Thompson et al. 2007) and support our broader term, subordinate predator release.

4.4 | Limitations

It is important to recognise that here we have only collated evidence for the potential occurrence of subordinate predator release between a pairing, without assessing studies that found no or a positive connection or mutual avoidance between those species. Jachowski et al. (2020) showed that there is contradicting or unclear evidence for many North America species pairs, and this is likely reflected globally. We emphasise that whilst a pair may have strong evidence for the potential for release, before any decisions are made based upon that, any contradictory studies need to be reviewed, especially in light of the context-dependency of carnivore interactions. We also acknowledge that some of the studies included may reflect competitor release rather than subordinate predator release, as we relied on the authors of each study's interpretation of their results. This could mean that some of the pairs could also show an increase in the species we have labelled as dominant if the species labelled as subordinate declined. However, pairs that are equally competitive are ecologically rare, and the recorded potential for release would still be accurate if the species labelled as dominant declined and therefore, this potential mislabelling does not impact the key takeaways from this review.

As discussed in our bias assessment, our search protocol may have introduced some bias; however, we believe this to be limited. The main limitation is the restriction to English publications, potentially leading to geographic bias. This could be the cause of the limited results from regions like North Asia and Central Africa rather than research effort. Additionally, while studies in other languages may alter pairs top rankings, the current data still highlight areas needing further research. We recommend those studying pairs ranked as strength 1 or strength 2 review non-English literature. We also acknowledge that while our review covers carnivores across trophic levels, it is restricted to terrestrial mammals, and similar processes may occur across other organism classes.

5 | Conclusion

Our review underscores the complexity of studying intraguild interactions and interpreting suppression. Evidence from various studies demonstrates that subordinate predator release can occur across a spectrum of trophic levels, challenging traditional trophic-based terminology. This complexity reveals that predator–predator relationships are not confined to species of similar sizes; rather, they can involve significant ecological impacts between species with considerable size and trophic differences. Such findings emphasise the need for community-wide approaches in researching interguild interactions and formulating conservation strategies. A broader perspective that encompasses these nuanced predator dynamics is essential for accurately understanding and managing predator populations and their ecological roles.

6 | Future Recommendations

We recommend that researchers and conservation practitioners avoid assumptions about a species' likelihood of experiencing release and ensure that conservation planning is grounded in local ecological evidence. Additionally, we propose two key avenues for future research to enhance the understanding of subordinate predator release globally. First, collating evidence that contradicts studies showing the potential for release will improve our understanding of the context dependency of intraguild interactions and the methodological challenges in studying these complex relationships. Second, analysing the strength of responses between studied species pairs will help conservationists and managers assess potential risks and ecological impacts.

Author Contributions

Emily K. Madsen: conceptualization, methodology, writing – review and editing, writing – original draft, investigation, formal analysis, data curation. **Shreya Ray:** validation, writing – review and editing, data curation. **Lisanne Petracca:** conceptualization, writing – review and editing. **Jan F. Kamler:** conceptualization, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.