



## The fox who cried wolf: A keywords and literature trend analysis on the phenomenon of mesopredator release



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### ARTICLE INFO

#### Keywords:

Mesopredator release  
Bibliometric analysis  
Food Webs  
Interspecific Interactions  
Canidae

### ABSTRACT

Human activities severely impact the distribution and behaviour of apex predators in numerous terrestrial and aquatic ecosystems, with cascading effects on several species. Mesopredator outbreaks attributable to the removal of an apex predator have often been recorded and described in the literature as “mesopredator release”. During recent decades several examples of the phenomenon have been observed and studied in many different parts of the world. In this paper, we quantitatively reviewed the existing literature on mesopredator release using two software packages (VOSviewer and CiteSpace) to investigate patterns and trends in author keywords through occurrences and temporal analyses, and creating relative network maps. The results showed that even though the general scientific interest in mesopredator release has increased in recent decades, the vast majority of studies focus on canid species, leaving many other species or entire taxa (e.g., reptiles) understudied and under-described. The connection between invasive species and mesopredator release has only recently been more extensively explored and also the effects of apex predators declining in aquatic ecosystems are still only partially investigated. Due to the increasing effect of biological invasions, overfishing, and either the decline or the rise of apex predators in different parts of the world, we expect an even higher increase in interest and number of published documents on the subject. We also encourage widening the research focus beyond canids to include other important taxa.

### 1. Introduction

Interspecific interactions represent a key component in the ecological and evolutionary dynamics of populations as they can affect communities, ecosystems, and food chains (Barbosa and Castellanos, 2005). Among all of them, predation and competition surely play a fundamental role in the interspecific dynamics of an ecosystem (Ripple et al., 2014; Ritchie and Johnson, 2009), being recognized as one of the major factors shaping community structure (Viota et al., 2012) and being, therefore, deeply investigated in the recent decades. Other interactions such as mutualism and commensalism, and parasitism remain, when involving carnivores, poorly considered and understood (Muhly et al., 2013; Saggiomo et al., 2017). Apex predators, in particular, have a prominent role in shaping the composition and the function of ecosystems affecting both sympatric competitors and prey (Ritchie and Johnson, 2009). Top predators can, for example, suppress herbivore populations (Ripple and Beschta, 2004) or affect the distribution and the

range of subordinate mesopredators (Creel and Christianson, 2008; Newsome et al., 2017; Palomares et al., 1996; Wysong et al., 2020). Already many decades ago, biologists began observing that the removal of a top predator from an ecosystem resulted in what Soulé defined as “mesopredator release” (Soulé et al., 1988), an increase in the number of smaller predators, and more intense predation on their prey. Today this hypothesis is defined, more generally, as the expansion in density or distribution, or the change in behaviour of middle-rank predators because of the decline in density or distribution of a top predator (Prugh et al., 2009). The relationships between apex and mesopredators also contemplate the opposite phenomenon. Thus, evidence of a reduction in mesopredators abundance when an apex predator returns to an ecosystem is present in literature. This reverse, yet related event is also of great importance as it can provide further and crucial implications related to, for example, the reintroductions of large carnivores (Jiménez et al., 2019).

Examples of mesopredator release have been observed and studied in

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several terrestrial ecosystems among mammals [e.g., lynx (*Lynx lynx*) and red fox (*Vulpes vulpes*) (Helldin et al., 2006), wolf (*Canis lupus*), and coyote (*Canis latrans*) (Merkle et al., 2009), lion (*Panthera leo*) and olive baboon (*Papio anubis*) (Prugh et al., 2009), coyote and opossum (*Didelphis virginiana*) (Rogers and Caro, 1998)], mammals and birds [e.g., coyote and common raven (*Corvus corax*) (Mezquida et al., 2006)], mammals and arthropods [e.g., raccoon (*Procyon lotor*) and ghost crab (*Ocypode quadrata*) (Prugh et al., 2009)], apex and mesoscavengers (O'Bryan et al., 2019), and also in aquatic ecosystems between fishes [e.g., large sharks and rays, skates, and small sharks (Myers et al., 2007)]. Cases of mesopredator release also involve exotic or invasive species, as shown in a study carried out in Tasmania which highlighted the negative impact of the facial tumour disease on the top predator -the Tasmanian devil (*Sarcophilus harrisii*)- populations, leading to the release of the alien mesopredator -feral cat (*Felis catus*) (Cunningham et al., 2020).

In contrast, a study from England documents how an increase in the dominant native Eurasian otter (*Lutra lutra*) resulted in a significant decrease in populations numbers of the invasive American mink (*Mustela vision*) (McDonald et al., 2007).

Over the last decade, researchers have focused their attention on climate change and its effects on the distribution and abundance of species, as well as their interactions (Elmhagen et al., 2017). Even though it has been documented that mammals -and carnivores in particular -are especially vulnerable to climate change (Rather et al., 2020), it is still unclear how they respond to it. Reactions to these changes may differ from one part of a species' range to another, and according to its interactions with other species (Pasanen-Mortensen et al., 2013). Of major concern is the observation that the changes affect the very existence of several mesopredator populations' dynamics in both marine and terrestrial ecosystems (Glass et al., 2021; Hempson et al., 2018). For example, while in arctic environments changes in snowfall frequency and abundance, and snow characteristics can affect mesopredators such as the wolverine (*Gulo gulo*) (Glass T.W. et al. 2021), the frequency and severity of drought may turn Australian small mammals into easier prey (Allen et al., 2018). Moreover, in marine ecosystems, modification of the reef biodiversity and structures, due to higher temperatures, can impact piscivorous mesopredators (Hempson et al., 2018).

Today, not only climate change, but human activities and infrastructure are also severely impacting the distribution and presence of apex predators (Gehr et al., 2017), both modifying their behaviours (Frey et al., 2020) and driving them to extinction in several terrestrial and aquatic ecosystems (Estes et al., 2011; Prugh et al., 2009; Strong and Frank, 2010). In the last 50 years, in the United States alone, the level of urbanization has more than doubled. Thus, loss of agricultural and natural areas has impacted several communities, with different species reacting differently (Prange and Gehrt, 2004). So far, even though urbanization heavily alters both marine and terrestrial environments, terrestrial urban ecosystems have been studied more intensively (Heery et al., 2018). High levels of urbanization have been observed to facilitate certain mesopredators by easing their access to food and shelter, therefore improving their survival and reproductive success (Heery et al., 2018). In addition, large carnivores are returning in the European countries (Boitani and Linnell, 2015; Trouwborst, 2010), and there is an increasing number of species thriving in non-native habitats (Pyšek et al., 2020). Moreover, the impact of the mesopredator release phenomenon goes beyond the conservation of ecosystems and also has strong economic (Packer et al., 2009; Prugh et al., 2009) and ethical implications (Jiménez et al., 2019; Trewby et al., 2008). In light of all this research, we consider the mesopredator release hypothesis as a rather important and topical matter to explore.

On a different note, the agreement on the reliability of the studies on mesopredator release is not unanimous, and the strength of the science in support of the hypothesis has been questioned in bulk of studies (reviewed in Allen et al., 2017). Specifically, factors such as the still-limited amount of evidence in support of it, the unreliability of

sampling methods for carnivores, the overlooking of alternative hypotheses, the logical fallacies in the literature, the lack of applied studies, and the extreme specificity of the ecosystems for which the mesopredator hypothesis has been validated may weaken its validity on a larger scale (Allen et al., 2017).

In this study, we investigated the global literature on the subject and we did not attempt to examine the reliability or accuracy of the actual science in the papers we reviewed.

The goal of this investigation is to explore the scientific literature on the mesopredator release phenomenon and identify patterns and trends in the scientific production focusing on the topic. For these reasons, we carried out a bibliometric analysis, a technique increasingly used in recent years, to quantitatively review the scientific literature across various disciplines (Buonocore et al., 2019; Otte and Rousseau, 2002; Pauna et al., 2019; Pauna et al., 2018; Skaf et al., 2020).

## 2. Materials and methods

We performed a bibliometric analysis of the scientific literature on the topic of mesopredator release using two different bibliometric techniques, i.e., bibliometric network analysis and citation burst analysis. The bibliometric network analysis was performed to quantitatively investigate and visualize through network maps the relationships among the research areas, while the citation burst analysis was instead used to identify fast-growing topics over time.

### 2.1. Data collection

To conduct the bibliometric analysis, we searched for published documents on the topic of mesopredator release in the Web of Science (WOS) database. The search was performed on the 19<sup>th</sup> of May 2020 and the research string TS= "Mesopredator Release" was used. We selected the time frame 1945-2020 and collected 376 papers. Results were exported selecting "Full Record and Cited References" as a plain text file format.

### 2.2. Bibliometric network analysis

The bibliometric network analysis of the literature on the topic of mesopredator release was carried out using VOSviewer (version 1.6.10) (Van Eck and Waltman, 2019), a software designed to create and visualize maps based on bibliometric data. To perform the analysis on the literature on mesopredator release, the author keywords were chosen as the item of investigation, and only the keywords used more than ten times were taken into account. The software generated network maps in which the frequency of occurrence of each keyword is proportional to the size of the corresponding network node and keyword font. The thickness of the connection lines between keywords was based on their "link strength", a link attribute expressed by a positive numerical value: the more two keywords simultaneously occurred in scientific publications, the thicker was the line linking them. Moreover, keywords that were often used together in scientific documents were grouped in the same cluster, with each cluster identified by a different colour. To estimate the real importance of a keyword in the network, we used a "thesaurus file" (Table S1) merging all the synonyms into one. In addition, the overlay visualization can be selected to deliver a temporal perspective on the network structure. In this case, items are coloured based on their average publication year (layout view), providing, therefore, information on how the network developed over time.

### 2.3. Citation burst analysis

To perform the citation burst analysis, we used CiteSpace, a software tool designed to perform scientometric analyses (Chen, 2006, 2017). Among its features, CiteSpace allows for the analysis of keywords that experienced an abrupt increase in the number of citations in a specified

period of time (i.e., a “citation burst”). The detection of the mentioned bursts is based on the Kleinberg algorithm (Chen, 2014). This algorithm, developed for the purpose of detecting bursts of single words and extract meaningful structures from documents (Kleinberg, 2003) can also be applied to multiword terms and citations of papers (Chen, 2006). For the purpose of this study, we analysed the burst in the author keywords, as well as in the “Keywords Plus” (i.e., keywords derived from the titles of cited references).

#### 2.4. Additional analyses

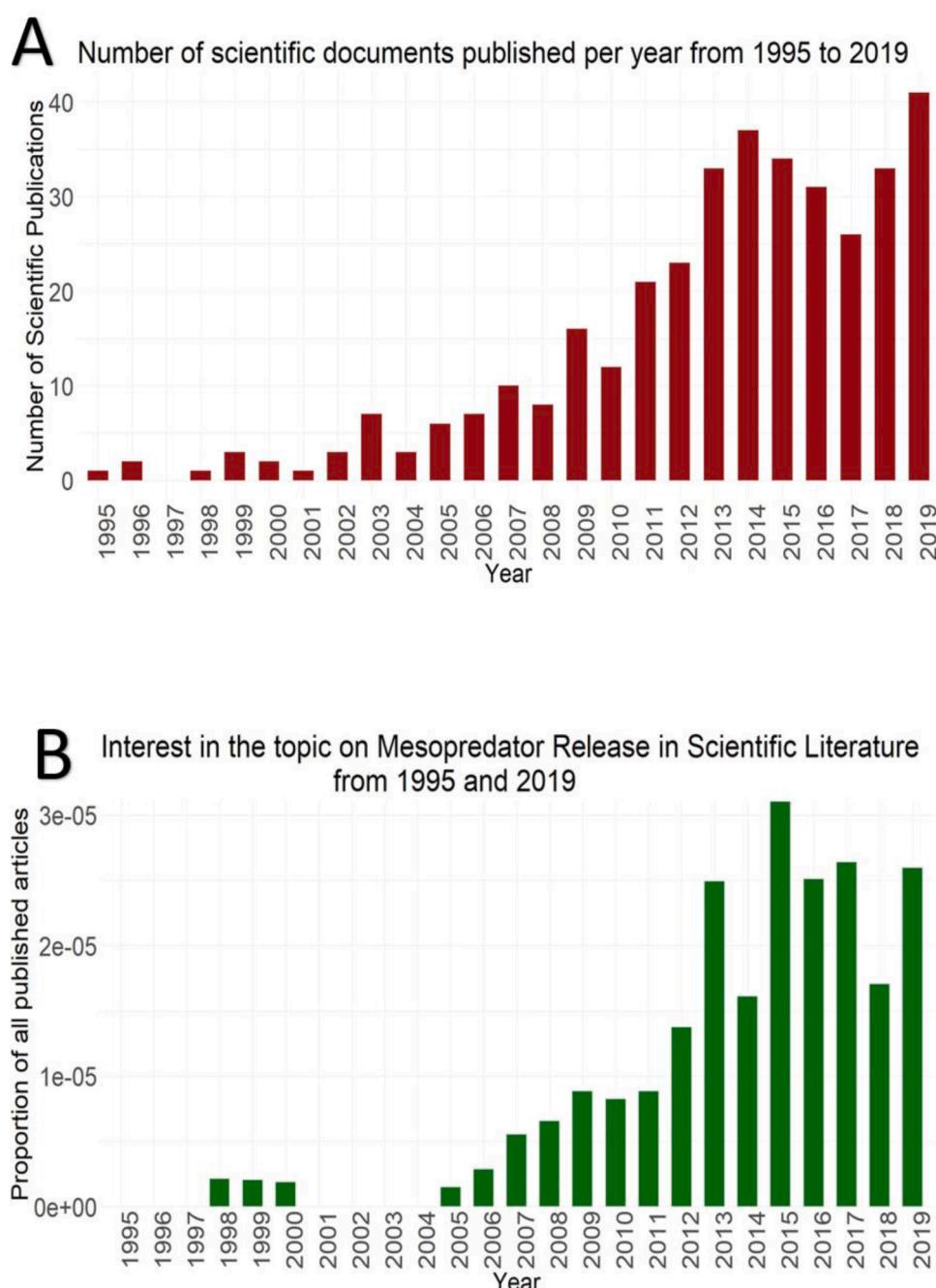
In addition to the two aforementioned analyses, the trend in the number of documents published per year (1995–2019) on the database “Web of Science” was investigated, as well as the trend in interest in the topic. The interest was defined as the ratio of the total number of papers

published in a year to the total number of published papers that discussed the topic of mesopredator release in the same year. This analysis was carried out using the Europe PMC database and the “europemc” package in R.

Information such as the percentages in the type of documents (i.e., article, review, editorial material, proceeding papers, early access, book chapter, meeting abstract) and research areas, as defined by WOS, was also analysed.

### 3. Results

The analysis of the number of documents published in the WOS database per year showed that starting with the first paper on mesopredator release published in 1995, the number of published documents on the subject increased fairly steadily with two peaks in the recent



**Fig. 1.** Temporal trends of publication of documents on mesopredator release (A) and of general interest on the subject (B).

decade (Fig. 1). Investigating the trend of interest on the subject as the ratio of all papers published in a year to all papers addressing the mesopredator release published in the same year, our results show that this value also increased with three peaks in 2013, in the timeframe 2015–2017 and 2019.

On a total of 376 documents (Supplementary Material File S1) on the subject listed on WOS, 83% were classified as articles and 8% as reviews. Just a small percentage of the documents fell under “editorial materials” or “other” (Fig. 2). The analysis of the WOS research areas (Fig. 3) showed that the majority of papers appeared in broad areas such as “Environmental Science ecology”, “Zoology” and “Biodiversity Conservation”. Even though water-related research areas (i.e., “Marine freshwater biology” and “Oceanography”) were listed, both contained a very small number of documents.

The most frequently mentioned keywords in the 376 scientific documents were “mesopredator release” and “trophic cascades” (Fig. 4). Among the top 20 keywords (Table 1), we found 5 species-specific scientific names and 1 common name. Among these, all but one (“*Felis catus*”) belonged to the family *Canidae*. The VOSviewer visualization map also showed four clusters: the first cluster, in red (composed of “Mesopredator”, “Biodiversity”, “Conservation”, “Predation”, “Carnivores”, “Competition”), the second cluster, in green (containing the keywords “apex predator”, “trophic cascade” and “mesopredator release”), the third cluster, in blue (including “*Vulpes vulpes*”, “*Canis lupus*”, “*Canis latrans*” and “Predator control”), and the fourth, in yellow (showing “*Canis lupus dingo*”, “fox”, “intraguild predation” and “mesopredator release hypothesis”).

The layout visualization (Fig. 5) showed that keywords such as “invasive species” and “biodiversity” have mostly appeared only recently, while “competition” and “carnivores” are not as strongly

present in the literature now as they were in the past. Results also show that “intraguild predation” is not often utilized in recent papers, while “species interaction” is.

The analysis of the citation bursts for the author keywords (Fig. 6) showed that the keyword “intraguild predation” had a burst of 5 years from 2009 to 2014, while the keyword “invasive species” had a burst in 2018. The analysis of “keywords plus” (Fig. 7), which also took into account the keywords of cited references, gave instead information on bursts in keywords related to more specific topics, such as “nest predation”, as well as very general ones such as “dynamics”, “community”, or “competition”.

#### 4. Discussion

According to the analyses of the number of publications per year, the number of documents on the topic had an increase until 2014, followed by a small decline (2015–2017) and by another increase (2018–2019). This is unsurprising given that the number of scientific journals has almost doubled (98% of increase) between 1998 and 2012 (Gu and Blackmore, 2016), with a consequent increase in the number of publications and active authors (Atae-Ashtiani, 2017; Bornmann and Mutz, 2015; Jinha, 2010; Mabe, 2003; Michels and Schmoch, 2012; Pautasso, 2012). Still, 85% of the existing documents on the topic were published between 2009 and 2019, even though the concept of mesopredator release was described in 1988, and the first document on the subject in the WOS database was published in 1995. Similarly, the overall interest in the topic increased, with more published documents on the subject in relation to the overall number of documents available.

Even though the phenomenon of mesopredator release can influence economic, social, and ecological values, the discussion of the subject

## Document types

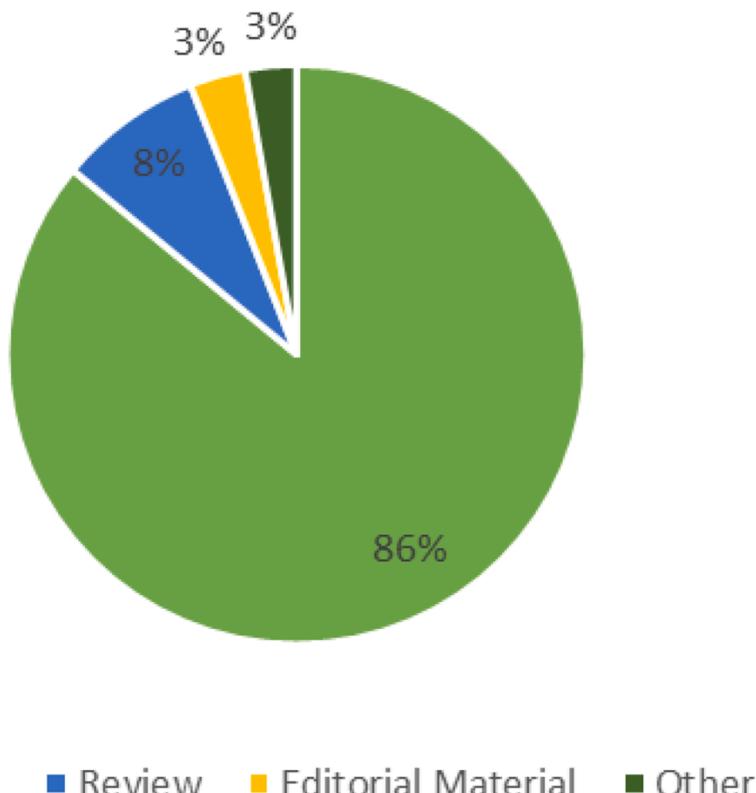
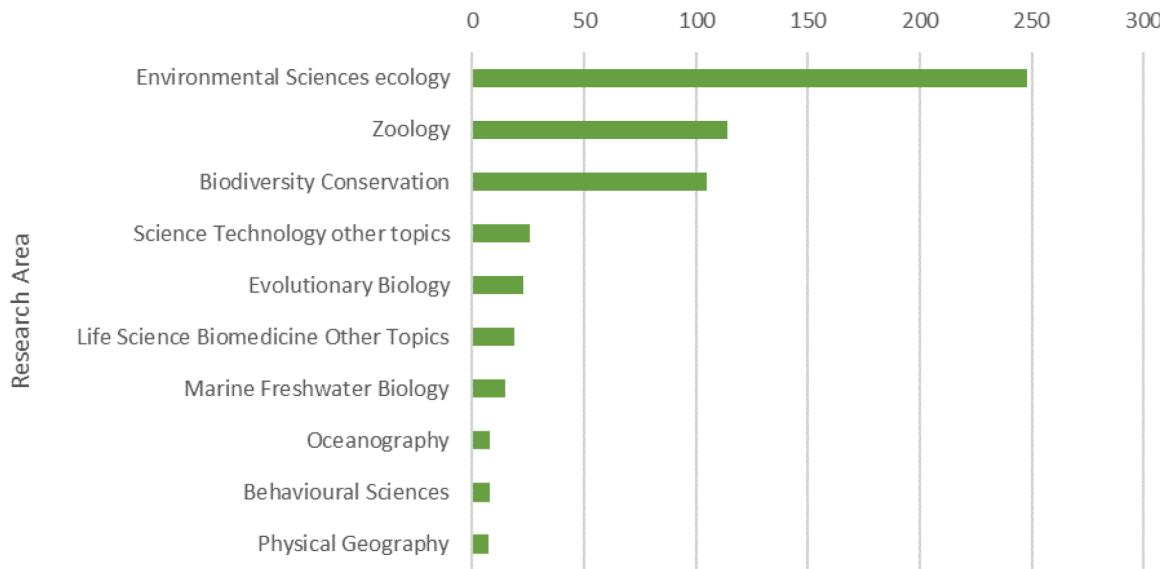
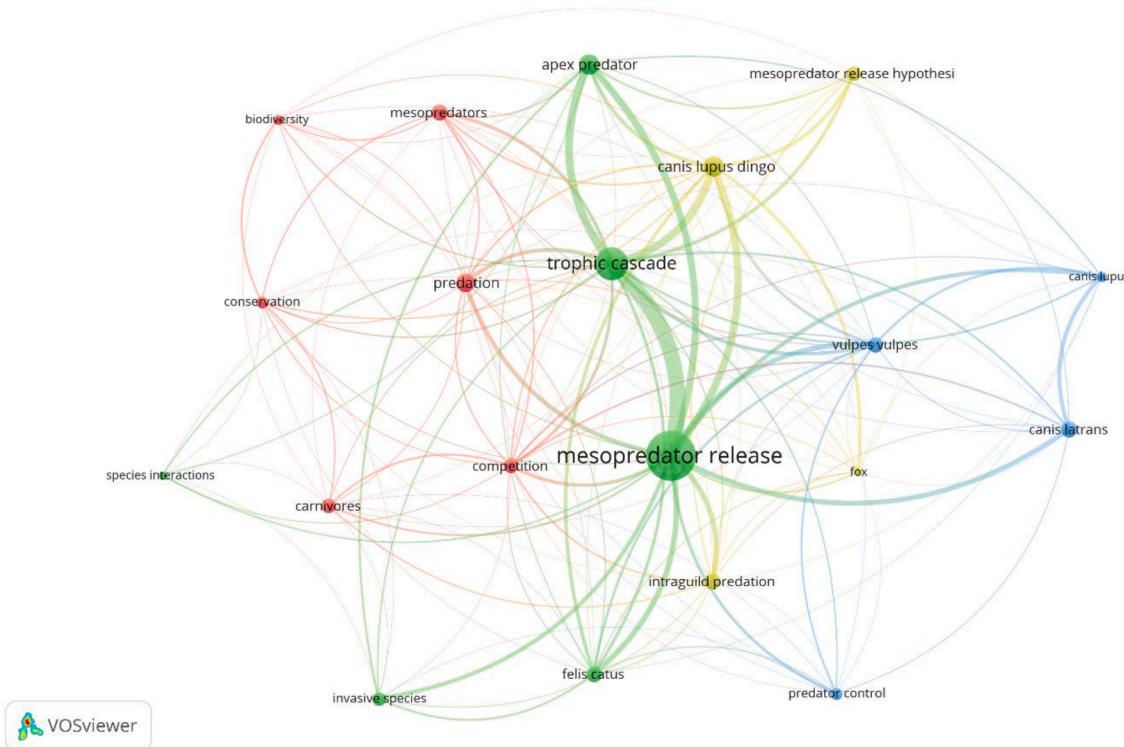


Fig. 2. Percentage of the types of published documents addressing mesopredator release from 1995 to 2020.



**Fig. 3.** Number of publications in the different WOS research areas from 1995 to 2020.



**Fig. 4.** Co-occurrence network map of author' keywords from documents published on the topic of mesopredator release from 1995 to May 2020.

focuses on ecological values, as indicated by the presence of “Environmental Science Ecology”, “Zoology” and “Biodiversity Conservation” in the top three list of the WOS research areas (Fig. 3). Several studies link conservation of biodiversity and mesopredator release (Courchamp et al., 1999; Nimmo et al., 2015; Ritchie and Johnson, 2009), focusing on the ecological roles of apex predators in the stabilization of ecosystems (Wysong et al., 2020), food webs (Ripple et al., 2014; Scoleri et al., 2020), and prey species (Wallach et al., 2015; Wysong et al., 2020).

The VOSviewer cluster visualization shows that keywords such as “*Vulpes vulpes*”, “*Canis lupus*”, “*Canis latrans*” and “Predator control” are often used together. Wolves are known to have a suppressive effect on the number of mesopredators [e.g., coyote (Berger and Gese, 2007;

Ripple et al., 2013)], keeping their numbers under control, while they seem to facilitate others [i.e., the red fox, facilitated both indirectly (Levi and Wilmers, 2012) and directly (Ferretti et al., 2021)]. The high proportion of studies on wolves and foxes, and the presence of these keywords among the frequently occurring keywords is unsurprising. Thus, both species are among the most widely distributed on the planet (Boitani, 2018; Hoffmann and Sillero-Zubiri, 2016).

The fox and coyote have close relationships with human environments (Doncaster et al., 1990; Fox, 2006; Gehrt and McGraw, 2007) being able to forage also on trash and pet food (Doncaster et al., 1990; Prugh et al., 2009) and to be found in close proximity to human activities (White and Gehrt, 2009). Moreover, both predators thrive in

**Table 1**

Top 20 most occurring author keywords in published documents on mesopredator release.

Keywords	Occurrence
Mesopredator release	95
Trophic cascade	57
<i>Canis lupus dingo</i>	32
Apex predator	31
Predation	28
Intraguild predation	23
<i>Canis latrans</i>	23
Mesopredators	23
<i>Vulpes vulpes</i>	22
<i>Felis catus</i>	22
Carnivores	21
Competition	20
Mesopredator release hypothesis	20
Invasive species	19
Conservation	17
Predator control	17
<i>Canis lupus</i>	14
Biodiversity	13
Species interactions	11
Fox	10

fragmented landscapes where apex predators struggle (Beasley et al., 2013; Crooks and Soulé, 1999; Prugh et al., 2009), and the proximity of foxes and coyotes with humans, together with the decline of wolf populations across the years (Berger et al., 2001; Flagstad et al., 2003; Jansson et al., 2012; Ripple et al., 2013; Wayne et al., 1992) has allowed an increase in numbers of the two species in densely urbanized areas. A well-aimed management strategy (i.e., “predator control”) is thus needed in order to avoid possibly dangerous interactions with humans and their pets (Alexander and Quinn, 2011; Baker and Timm, 1998; Lukasik and Alexander, 2011), and to reduce the conflict with human activities as much as possible (Moberly et al., 2004) (Ritchie and Johnson, 2009; Thorn et al., 2012).

The fourth cluster, instead, suggests a link between “*Canis lupus dingo*” and “Fox” which are both recognized as mesopredators, so their presence in the same cluster of the keyword “intraguild competition” is

unsurprising.

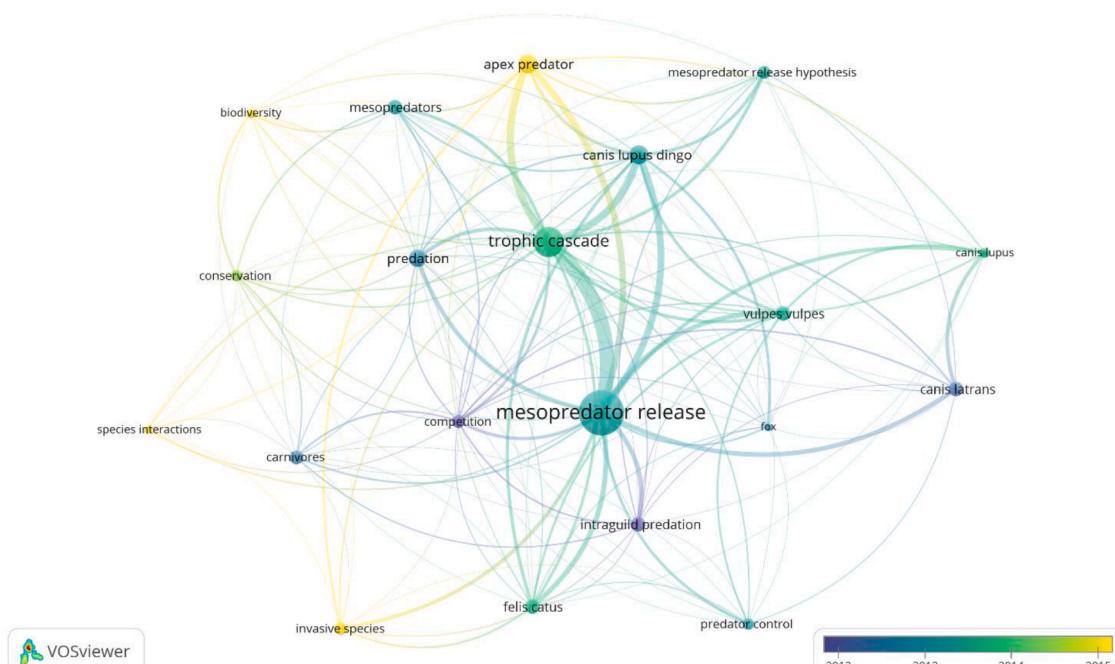
The vast majority of studies focused on the phenomenon of mesopredator release come from the description of *Canidae* interactions (Gehrt and Clark, 2003; Knowlton et al., 1999) and their impacts on ecosystems, as shown from the presence of five species of canids in the first 20 keywords. As a result, other important taxa are surely overlooked. Thus, as it has already been observed by Nowak et al. (2008) and by Sutherland et al. (2011), reptiles are generally excluded by studies regarding top predator/mesopredators dynamics, even though they exercise a major predatory influence in many ecosystems. Similarly, birds are not often included in the literature even though examples of mesopredator release affecting them are known (Rees et al., 2019; Suraci et al., 2014). Last, cases of mesopredator release involving species of fishes have also been documented (Christie et al., 2020; Myers et al., 2007; Ritchie and Johnson, 2009) and, despite the increasing effects of overfishing that is now reducing the number of marine apex predators (Hammerschlag, 2019; Myers et al., 2007), they seem to be still overlooked when considering the global production on the topic of mesopredator release.

Among the 20 most common keywords, it is interesting that there is only one non-canid species “*Felis catus*”, at the tenth place. This result may be due to the increased interest in management strategies designed to limit the massive impact of this felid on local wildlife (Mori et al., 2019; Seymour et al., 2020). Domestic cat distribution and densities are thought to reflect human densities and their penchant for keeping them

## Top 2 Author Keywords with the Strongest Citation Bursts

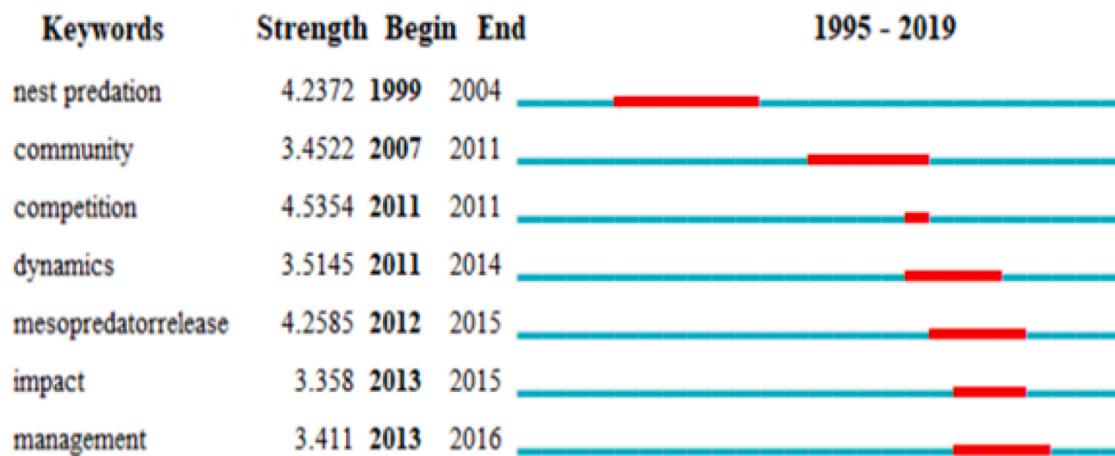


**Fig. 6.** Citation burst analysis of author keywords in published documents on mesopredator release. For each keyword, the strength of the burst (minimum 1 year) and the time span are showed.



**Fig. 5.** Overlay of time-dependence on the visualization map of the Co-occurrence network of author keywords from documents published on the topic of the mesopredator release from 1995 to May 2020.

## Top 7 Keywords Plus with the Strongest Citation Bursts



**Fig. 7.** Citation burst analysis of keywords plus in published documents on mesopredator release. For each keyword, the strength of the burst (minimum 1 year) and the time spawn are showed.

as pets (Sims et al., 2008). Domestic cats are often left free to roam and explore (Mori et al., 2019) and, in addition, the number of feral cats is rising (Trouwborst et al., 2020) in many countries including Canada (Blancher, 2013), the United States (Loss et al., 2013), Australia (Woinarski et al., 2018; Woinarski et al., 2017), New Zealand (Loss and Marra, 2017), the Netherlands (Knol, 2015; as in Trouwborst, 2010), the United Kingdom (Woods et al., 2003), Poland (Krauze-Gryz et al., 2019), Belgium, and France (Pavis et al., 2019). These populations are still being poorly managed (cfr. Trouwborst et al., 2020), even though they represent a huge threat to both insular (Doherty et al., 2016; Hervías et al., 2014; Nogales et al., 2013) and mainland (Mori et al., 2019) ecosystems, representing a major threat in terms of killing birds, mammals, reptiles, amphibians, fish, and invertebrates (Mori et al., 2019; Trouwborst et al., 2020) when not controlled or suppressed by an apex predator (Crooks and Soulé, 1999).

The layout visualization shows a recent increase in the occurrence of the keywords “biodiversity” and “conservation”, suggesting that research on mesopredator release, though still linked to species-specific cases (e.g., Canids), is now headed to a more conservation-aimed approach.

The interest in the topic of invasive species is also growing, as shown by the layout visualization and confirmed by the analysis of author keyword bursts (Fig. 6). Conversely, the analysis of the “keywords plus” (Fig. 7) shows that the keyword “management” is also used only rather recently. Considering the increasing interest in this topic in the current literature, the worldwide disappearance of apex predators or the return of others in their old ecosystems, and the increasing number of invasive species spreading in non-native habitats, we expect a boost in the number of studies focused on this topic and its related effects in the upcoming years.

### 5. Conclusions

In this study, we analysed keyword and literature trends on the phenomenon of mesopredator release.

Our study pointed out that the number of documents on the topic has significantly increased in recent decades, with sharper peaks in the last ten years, as well as the general interest in the subject. As the topic has several economic and ecological repercussions, we attributed this increased interest to a forced re-evaluation of the role of apex predators in shaping ecosystems and their food webs, and to the threats to

biodiversity conservation and prevention of wildlife-human conflicts deriving from their disappearance.

The recent presence of the domestic cat in the list of the ten most occurring keywords may represent a recent need for a biodiversity conservation plan aimed at this invasive species. Its presence may, in fact, be connected to the devastating reductions in the local wildlife mostly in ecosystems lacking apex predators that might have kept domestic cat populations under control. This situation is made even more urgent by the estimated number of domestic cats in the world, which reaches the amount of 370 million (data from 2018, Bedford, 2020), and by the fact that a high percentage of them are left free to roam outdoors in many countries around the world (Foreman-Worsley et al., 2021).

Mammals, especially Canids, and interactions amongst them, still seem to be the most investigated context of the phenomenon. Particular attention is given to coyote and fox, two species that thrive in human-dominated landscapes and with whom a conflict may, therefore, more commonly arise.

The downside of the prevalence of the Canids among the most studied species is the overlooking of the interactions and the effects of mesopredator release on other, equally important taxa (e.g., reptiles, fishes) and related problematics, but the large number of canid studies may represent a foundation for further investigations and to be referred to also for investigating other contexts and species.

Considering the return of apex predators in many ecosystems and the disappearance of them in others, studies aimed to better understand this phenomenon also across ecosystems and mesopredator species so far overlooked including reptiles, birds, and fish, are clearly needed.

### Declaration of Competing Interest

The authors certify that they have NO affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

## Acknowledgment

This study was supported by the Internal Grant Agency of the Faculty of Forestry and Wood Sciences (Czech University of Life Sciences) project A\_19\_31 to LS, and the Ministry of Agriculture of the Czech Republic, institutional support MZE-RO0718 to BE.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecocom.2021.100963.

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