


REVIEW, EDITOR'S CHOICE

Identifying mesopredator release in multi-predator systems: a review of evidence from North America

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ABSTRACT

1. The mesopredator release hypothesis, defined as the change in distribution, abundance or behaviour of a middle-ranking predator in response to a decrease in density or distribution of an apex predator, is an increasingly popular topic in ecology. Terrestrial mesopredators have been reported as being released in multiple systems globally, particularly in North America, over the past century.
2. We reviewed 2687 scientific articles, of which we determined that 38 met our criteria for investigating mesopredator release (MR) in terrestrial North American mammalian predators.
3. We observed no support or mixed support for MR in 46% of all relevant studies, including conflicting evidence between measures (mesopredator distribution, abundance or behaviour) within a given study and among studies of the same community in different settings.
4. To advance the study of MR, we provide a conceptual framework that 1) highlights the multiple spatial, temporal and ecological scales at which mesopredator responses can occur; 2) suggests the relative weight of evidence for MR that is provided by measures of mesopredator responses at each scale; and 3) clearly defines the threshold for determining when MR is occurring.
5. In increasingly reshuffled predator communities with declining apex predators, there is a need for future studies to assess in more detail the contexts in which mesopredator behavioural responses scale up to the population-level processes and species-level distribution changes needed to identify these responses as MR.

INTRODUCTION

The mesopredator release hypothesis, defined as the change in distribution, abundance or behaviour of a middle-ranking predator in response to a decrease in density or distribution of an apex predator (Prugh et al. 2009, Brashares et al. 2010), is an increasingly popular topic in ecology. Since

the phrase 'mesopredator release' was coined by Soule et al. (1988), literature containing the phrase (as well as the associated phrase mesocarnivore release; both phrases are hereafter collectively termed MR) has increased dramatically; MR was mentioned in over 64 scientific articles in 2018 alone (Fig. 1). Evidence for MR has been reported globally from a wide range of taxa, ranging from oceanic

benthic fish (Carscadden et al. 2001) to desert canid communities (Ralls & White 1995), leading some to conclude that the loss of apex predators “has created outbreaks of mesopredator populations throughout the world” (Prugh et al. 2009, p. 789).

Mesopredator release has received increasing levels of attention because of its potential cascading impacts on ecosystem functions. Evidence of MR is used to support the conservation or restoration of apex predators as a possible means of suppressing exotic or undesirable mesopredators (Brashares et al. 2010). Further, these top-down effects are often thought to extend beyond the predator community to prey and vegetation (Soulé et al. 1988, Terbough et al. 2001). For example, in one of the most frequently cited papers on MR, Rogers and Caro (1998) provide evidence to suggest that when coyotes *Canis latrans*, apex predators in the system, were absent, song sparrow *Melospiza melodia* nest success tended to be lower, potentially due to higher abundance of and predation rates by raccoons *Procyon lotor*, mesopredators. In addition, high economic, social and health costs for humans have been attributed to the cascading ecological effects of expanding mesopredators (Prugh et al. 2009, Brashares et al. 2010). Thus, MR has the potential to be a broad, ecologically important rationale for restoring apex predators to a landscape.

Historical and recent evidence suggests that MR is not universal following large predator removal, even among systems with similar species assemblies. Historically,

mammalian predator communities underwent a major reshuffling towards the end of the Pleistocene, 13.8–11.4 thousand years ago, when the loss of 80% of terrestrial megaherbivores (herbivore >1000 kg) and 20% of apex hyperpredators (predators whose diet consists of >80% meat) occurred (Smith et al. 2016, Van Valkenburgh et al. 2016). However, this dramatic loss of megaherbivores and apex predators did not universally result in a release of lower-ranking predators. For example, in North America, loss of megaherbivores and competition with humans probably kept remnant extant predators (jaguar *Panthera onca*, mountain lion *Puma concolor*, grey wolf *Canis lupus* and grizzly bear *Ursus arctos horribilis*) from expanding into niche space vacated by large hyperpredators (sabre-toothed cat *Smilodon fatalis*, scimitar-toothed cat *Homotherium serum*, dire wolf *Canis dirus* and short-faced bear *Arctodus simus*; Pardi & Smith 2016). More recently, conflicting evidence exists about the role of Australian dingoes *Canis lupus dingo* in limiting non-native red fox *Vulpes vulpes* and feral cat *Felis catus* populations, and in facilitating the recovery of endangered native rodent species (Johnson et al. 2007, Letnic et al. 2009, Allen et al. 2013). Similarly, there is ongoing debate about the MR-related suppression of raccoons by coyotes in North American systems, leading some to fear that “because of its intuitive appeal, conservationists and managers may defer to MR hypothesis despite the absence of supporting data” (Gehrt & Clark 2003, p. 840). At the very least, it

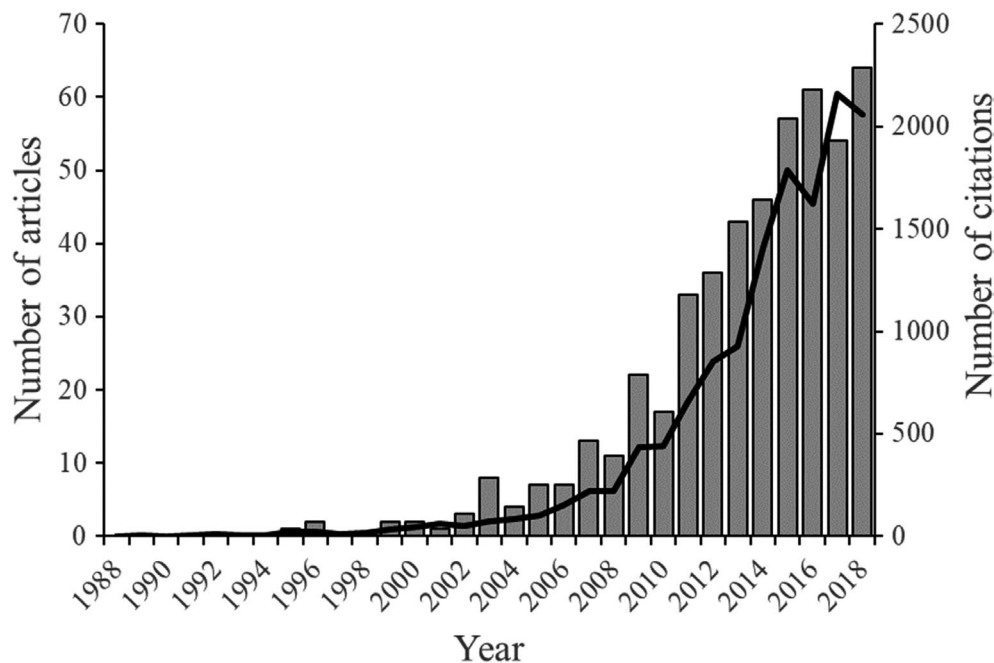


Fig. 1. Number of articles published (bars) and associated citations (line) per year involving the topic of mesopredator release, based on a Web of Science search performed on 4 February 2020, using the topic search: TS=(mesopredator OR mesocarnivore) AND (release OR competition OR “interspecific interaction” OR competition OR “trophic cascade” OR interguild OR intraguild).

is evident that not all mesopredators are being released where large predators have declined, and several are critically endangered (e.g. black-footed ferret *Mustela nigripes*, Darwin's fox *Lycalopex fulvipes* and Borneo bay cat *Catopuma badia*; IUCN 2018). Collectively, this and other competing lines of evidence suggest that the occurrence of MR is likely to be context-dependent (Haswell et al. 2017) and that an objective framework is needed for defining and evaluating the extent to which MR is occurring.

In this review, we evaluate the extent to which evidence supports the widespread occurrence of MR previously reported in North America. Based on our findings, we provide a novel conceptual framework that accounts for the various spatial, temporal and ecological scales at which mesopredators can respond to a decline in higher-ranking predators. We also offer a more precise definition of MR that identifies a threshold at which MR occurs based on the weight of evidence across these three scales of interspecific competition. Finally, we provide suggestions for improving future investigations into MR and discuss the conservation implications of broadly applying MR theory without considering the complexity of mesopredator responses.

METHODS

We reviewed scientific literature to evaluate the extent to which past studies of terrestrial North American mesopredator distributional, abundance and behavioural responses supported or did not support MR following discrete changes in apex predator abundance or distribution. We selected North American terrestrial mammalian predators for two reasons. First, similar to most other regions of the world, North America underwent a reduction of large mammalian predators in the 19th and early 20th Centuries (Ripple et al. 2014). Second, a previous review (Prugh et al. 2009) used evidence from North American mammalian mesopredator responses to losses of apex predators as evidence of the widespread occurrence of MR. Specifically, Prugh et al. (2009) estimated that, based on comparisons of current and historical ranges, 60% of mesopredator ranges in North America had expanded (an indication they interpreted as MR), and all apex predator ranges had contracted.

For each terrestrial mammalian predator species in North America, we searched for evidence of MR in Web of Science on 4 February 2020 using the following search phrase: TS=("scientific name" AND (competition OR "interspecific interaction" OR intraguild OR interguild OR trophic cascade OR "mesocarnivore release" OR "mesopredator release")). We discovered that these search terms resulted in many studies that indirectly evaluated interspecific competition,

such as studies of spatial overlap where multiple predators co-occur. Therefore, because MR requires a discrete change in apex predator distribution or abundance following which mesopredators respond (Brashares et al. 2010), we developed two restriction criteria for inclusion in our review. Studies were included which 1) included the simultaneous monitoring of both an apex predator and a mesopredator, or included ≥ 2 mesopredators provided that the interaction between the two showed clear trophic order differentiation necessary for MR (in the latter case, we refer to the higher-order mesopredator as the apex predator) and 2) observed variability over time in apex predator distribution or abundance within their geographical range (e.g. pre- vs. post-apex predator removal, recovery and reintroduction), or had discrete areas within or among the study area(s) where there were known, sustained (≥ 1 year) differences in apex predator distribution or abundance. This precluded short-term studies that documented fine-scale spatial or temporal variability in apex predator occurrence within a study area (such as variance in apex predator activity that occurred daily or seasonally), but did not provide evidence to suggest that those patterns were sustained over time, to result in the differential apex predator abundance or distribution needed to allow MR. Lastly, using a snowball sampling approach, we augmented this search with additional studies discovered during our review that did not appear in our original search.

For each study that met both our criteria for inclusion in this review, we assessed each apex- and second-order predator species pairing for evidence of support for MR based on measures of mesopredator distribution, abundance or behaviour. For example, if the apex predator was removed in a study and the associated response was an increase in abundance of the paired mesopredator, then we interpreted that study as providing support for MR. On occasions where three orders of predators were studied, we expected the third-order predator to exhibit the opposite trend to the second-order predator in response to apex predator treatments (e.g. when the apex predator is removed, the third-order mesopredator should be suppressed by the 'released' second-order mesopredator; St-Pierre et al. 2006). We defined support as conflicting or mixed within a response measure when there was variability among scales or multiple metrics of a measure (e.g. behavioural metrics of home range size and diet differed in their support of MR). We grouped behavioural responses of mesopredators to changes in apex predator distribution or abundance into three categories: activity (e.g. temporal activity patterns and foraging behaviour), diet (e.g. dietary overlap and shifts in diet) and habitat use (e.g. spatial avoidance and resource selection). Finally, we defined studies as either experimental or correlational. We defined studies as experimental if there was either 1) temporally

distinct pre- vs. post-treatment phase before and after the decline (e.g. killing and disease outbreak) or rise (e.g. reintroduction) of an apex predator at an individual study site, or 2) spatially replicated treatment vs. control design across two or more sites with differing levels of apex predator occurrence or abundance. We defined all other studies as correlational, given that they typically assessed trends in apex and mesopredator distribution or abundance over time without spatial or temporal replicates that represented the discrete gain or loss of apex predators.

RESULTS

Of the 2687 papers identified using our Web of Science search, 153 met our first criterion, and 36 of those met our second criterion for inclusion in this review (Fig. 2). Our snowball sampling resulted in two additional papers not found in our original search, resulting in a total of 38 papers for use in our systematic review. The majority of studies gauged the abundance responses of mesopredators (60%, $n = 23$), followed by behavioural responses (53%, $n = 20$), and changes in distribution (9%, $n = 2$). Seven studies (21%) investigated more than one response measure (i.e. distribution, abundance or behaviour) in the same study. Fourteen of the 38 studies (37%) employed an experimental approach, and the rest made inferences based on correlations. Over a quarter of the studies we reviewed (29%, $n = 11$) evaluated three trophic orders within a mammalian predator guild, and just over a third (37%, $n = 14$) examined pairwise interactions between more than two predator species in a system (Fig. 3).

Distribution and abundance

A majority (66%) of studies we evaluated assessed variation in mesopredator abundance or distribution in relation to changes in the abundance or distribution of an apex predator (Table 1). Most studies were based on correlation (64%, $n = 16$) rather than experimental manipulation (36%, $n = 9$). Studies that used an experimental approach typically measured the abundance or distribution of mesopredators on replicate sites with defined treatments of high and low apex predator abundance. Site treatments were directly assigned by killing the apex predator (12%, $n = 3$), or defined *a priori* based on predator hunting regimes or known distribution of the apex predator (20%, $n = 5$).

Studies assessing distribution or abundance changes generally supported the MR hypothesis. Within the 25 studies, authors investigated numerical relationships between an apex predator and second-order predator 34 times, which could be categorised into 17 distinct species pairings (Table 1). Across all 34 species pairings, 56% of species interactions indicated support for MR, 24% of species interactions indicated no support for MR, and 20% of species interactions indicated mixed or conflicting support within an individual study (Table 1). Three of the mixed support studies provided support for MR at larger spatial scales, but no support or inconclusive evidence at smaller scales (Thompson & Gese 2007, Guillaumet et al. 2015, Sivy et al. 2017).

Studies that investigated changes in distribution or abundance of mesopredators in relation to changes in apex predators were taxonomically biased towards canid species. Of the 34 species comparisons, 56% ($n = 19$) investigated

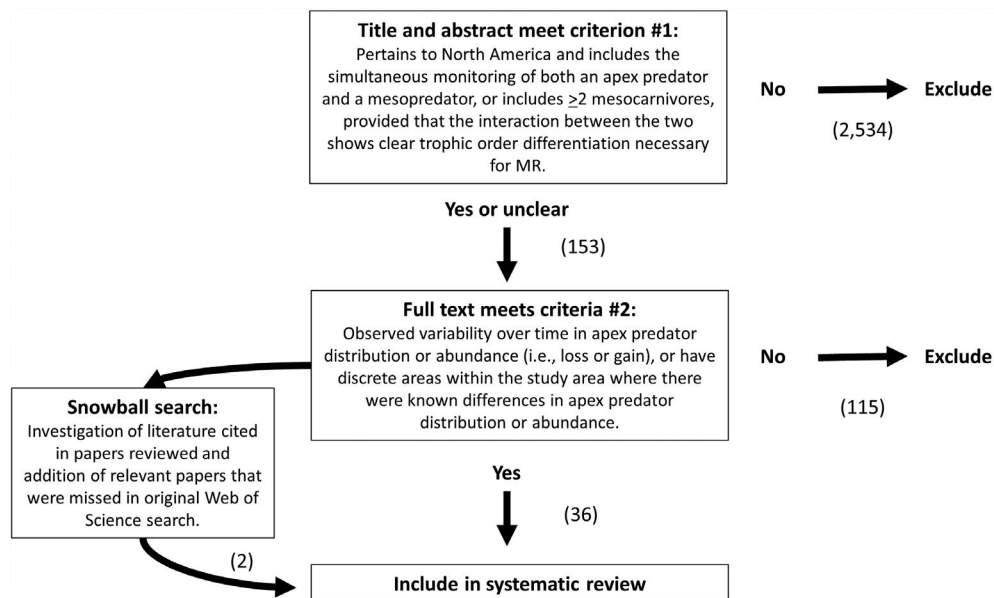


Fig. 2. Flow chart illustrating the process by which we reviewed and filtered articles for use in this review. Numbers in parentheses represent the number of articles retained or removed at each step in the process.

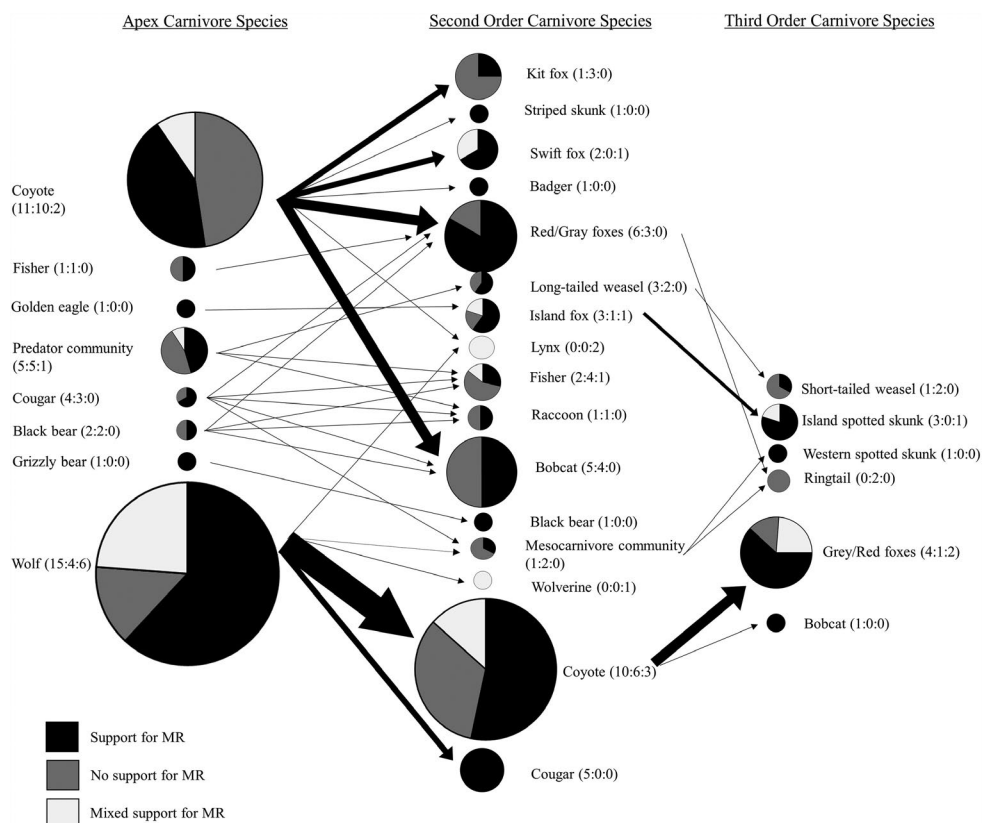


Fig. 3. Interaction web summarising studies of mesopredator release included in this review of terrestrial mammalian North American predators. Pie chart size reflects the number of studies that investigated a species in a specified trophic role (apex, second-order or third-order predator). Pie charts show the proportion of studies that suggested support, no support or mixed support for mesopredator release, and the numbers in parentheses indicate the number of studies that met each of these criteria, respectively. Evidence was categorised into three response metrics (distribution, abundance and behaviour; see Tables 1 and 2), and these metrics were not mutually exclusive within studies. Arrows are weighted to indicate the number of studies that investigated a pairwise interaction.

relationships between two canid species, and 76% ($n = 26$) treated coyotes as either an apex or a second-order predator (Table 1). While only eight studies did not include coyotes, all eight of those studies found support (63%) or mixed support (37%) for MR. By contrast, 46% of coyote studies observed no support or mixed support for MR, and of those 12 studies, a majority ($n = 8$) considered coyotes as the apex predator in the system under investigation (Table 1).

Cascading effects of MR onto a third-order predator species (i.e. >2 trophic levels) were rarely tested ($n = 7$ studies). Although six of these studies found support for cascading trophic effects indicative of MR, most (four of six) were related to secondary effects of coyote—grey wolf interactions (Table 1), providing further evidence of the strong taxonomic bias in the literature.

Behaviour

The majority of behavioural metrics evaluated for apex–mesopredator species pairings were activity metrics (50%,

$n = 18$), followed by diet metrics (28%, $n = 10$), and habitat use metrics (22%, $n = 8$; Table 2). For the 20 behavioural studies we reviewed (several of which measured multiple behaviour metrics), nine studies (45%) used an experimental approach where replicate sites were defined by the presence or absence of an apex predator, or active removal of an apex predator.

Across all behavioural categories and species pairings, 52% of species interactions indicated support for MR, 41% of species interactions indicated no support for MR, and 7% of species interactions indicated mixed or conflicting support within an individual study (Table 2). The most support for MR came from studies assessing changes in activity metrics ($n = 22$): 59% of evaluated species pairings provided support for MR, and 41% of pairings provided no support. The majority of species pairings assessing changes in diet ($n = 13$) found mixed support for MR: 46% of studies provided support for release, 46% of studies provided no support, and 8% provided conflicting support (Table 2). Studies that evaluated habitat use

Table 1. Summary of evidence for mesopredator release in North American terrestrial carnivores based on the observed change in mesopredator distribution or abundance in response to a change in the distribution or abundance of an apex predator in a given system. Evidence of release was determined based on the study authors' interpretation of their data. When multiple metrics for a common variable differed in supporting or not supporting mesopredator release within a study, we termed that study as providing mixed support. Species represented include badger *Taxidea taxus*, bobcat *Lynx rufus*, coyote *Canis latrans*, grey fox *Urocyon cinereoargenteus*, grey wolf *Canis lupus*, fisher *Pekania pennanti*, golden eagle *Aquila chrysaetos*, island fox *Urocyon littoralis*, island spotted skunk *Spilogale gracilis amphialus*, kit fox *Vulpes macrotis*, long-tailed weasel *Mustela frenata*, lynx *Lynx canadensis*, raccoon *Procyon lotor*, red fox *Vulpes vulpes*, striped skunk *Mephitis mephitis*, swift fox *Vulpes velox* and wolverine *Gulo gulo*

Measured response	Evidence of release						Citations
	Apex predator	2nd order predator	3rd order predator	Support	No support	Mixed support	
Abundance	Coyote	Badger	-	1	0	0	Henke and Bryant (1999)
	Coyote	Bobcat	-	2	2	0	Litvaitis and Harrison (1989)*,§, Henke and Bryant (1999)*,¶, Main et al. (1999)†,§, Fedriani et al. (2000)†,§
Distribution	Coyote	Grey fox	-	2	1	0	Henke and Bryant (1999)*,¶, Main et al. (1999)†,§, Fedriani et al. (2000)*,§
	Coyote	Kit fox	-	1	2	0	Cypher and Spencer (1998)†,§, White et al. (2000)*,§, Arjo et al. (2007)†,§
Abundance	Coyote	Lynx	-	0	0	1	Guillaumet et al. (2015)
	Coyote	Raccoon	-	0	1	0	Main et al. (1999)
Distribution	Coyote	Striped skunk	-	1	0	0	Henke and Bryant (1999)
	Coyote	Swift fox	-	2	0	1	Kamler et al. (2003)*,¶, Karki et al. (2007)*,¶, Thompson and Gese (2007)*,§
Abundance	Grey wolf	Coyote	-	1	1	1	Carbyn (1982)*,§, Berger et al. (2008)†,¶, Sivy et al. (2017)†,¶
	Grey wolf	Coyote	Fox (red and grey)	4	0	1	Dekker (1989)*,§, Levi and Wilmers (2012)*,§, Newsome and Ripple (2015)*,§, Flagel et al. (2016)*,¶, Crimmins and Van Deelen (2019)†,§
Abundance	Grey wolf	-	Red fox	0	0	1	Sivy et al. (2017)
	Grey wolf	Lynx	-	0	0	1	Sivy et al. (2017)
Distribution	Grey wolf	Wolverine	-	0	0	1	Sivy et al. (2017)
	Island fox	Island spotted skunk	-	1	0	0	Jones et al. (2008)
Abundance	Golden eagle	Island fox	Island spotted skunk	1	0	0	Roemer et al. (2002)
	Predator community	Long-tailed weasel	Ermine	1	0	0	St-Pierre et al. (2006)
Abundance	Predator community	Raccoon	-	1	0	0	Suraci et al. (2014)
	Grey wolf	Coyote	-	0	1	0	Berger and Gese (2007)
Distribution	Predator community	Fisher	-	1	0	0	Lapoint et al. (2015)

*Support for mesopredator release (MR) hypothesis.

†No support for MR.

‡Mixed support for MR.

§Correlational study.

¶Experimental study.

Table 2. Summary of evidence for mesopredator release in North American terrestrial predators based on the observed change in mesopredator behaviour in response to a change in the distribution or abundance of an apex predator in a given system. Evidence of release was determined based on the study authors' interpretation of their data. When multiple metrics for a common behaviour differed in supporting or not supporting mesopredator release within a study, we termed that study as providing mixed support. Species represented include black bear *Ursus americanus*, bobcat *Lynx rufus*, coyote *Canis latrans*, ermine *Mustela erminea*, grey fox *Urocyon cinereoargenteus*, grey wolf *Canis lupus*, grizzly bear *Ursus arctos*, fisher *Pekania pennanti*, golden eagle *Aquila chrysaetos*, island fox *Urocyon littoralis*, island spotted skunk *Spilogale gracilis amphialus*, kit fox *Vulpes macrotis*, long-tailed weasel *Mustela frenata*, lynx *Lynx canadensis*, mountain lion *Puma concolor*, raccoon *Procyon lotor*, red fox *Vulpes vulpes*, ringtail *Bassariscus astutus* and western spotted skunk *Spilogale gracilis*

Behaviour	Apex predator	2nd order predator	3rd order predator	Evidence of release			Study design	Citations
				Support	No support	Mixed support		
Activity	Black bear	Bobcat	-	1	0	0	Experimental	Allen et al. (2015)
	Black bear	Coyote	-	0	1	0	Experimental	Allen et al. (2015)
	Black bear	Fisher	-	0	1	0	Experimental	Allen et al. (2015)
	Black bear	Grey fox	-	1	0	0	Experimental	Allen et al. (2015)
	Predator community	Long-tailed weasel	-	1	0	0	Experimental	St-Pierre et al. (2006)
	Predator community	Long-tailed weasel	Ermine	0	1	0	Experimental	St-Pierre et al. (2006)
	Coyote	Bobcat	-	0	1	0	Correlational	Litvaitis and Harrison (1989)
	Grey wolf	Coyote	-	3	1	0	Correlational, Experimental	Atwood and Gese (2008) ^{†,¶} , Merkle et al. (2009) ^{*,§} , Miller et al. (2012) ^{*,§} , Shores et al. (2019) ^{*,¶}
	Grey wolf	Coyote	Bobcat	1	0	0	Experimental	Shores et al. (2019)
	Grizzly bear	Black bear	-	1	0	0	Experimental	Schwartz et al. (2010)
Diet	Island fox	Island spotted skunk	-	0	1	0	Correlational	Jones et al. (2008)
	Mountain lion	Coyote	-	0	1	0	Experimental	Allen et al. (2015)
	Mountain lion	Bobcat	-	1	0	0	Experimental	Allen et al. (2015)
	Mountain lion	Fisher	-	1	0	0	Experimental	Allen et al. (2015)
	Mountain lion	Grey fox	-	1	0	0	Experimental	Allen et al. (2015)
	Mountain lion	Mesopredator community	Western spotted skunk	1	0	0	Experimental	Allen et al. (2015)
	Mountain lion	Mesopredator community	Ringtail	0	2	0	Experimental, Correlational	Allen et al. (2015) [¶] , Byerly et al. (2018) ^{†,§}
	Grey wolf	Mountain lion	-	1	0	0	Correlational	Kortello et al. (2007)
	Coyote	Kit fox	-	0	1	0	Correlational	Cypher and Spencer (1998)
	Coyote	Bobcat	-	1	0	0	Correlational	Litvaitis and Harrison (1989)
Diet	Coyote	Red fox	-	1	1	0	Correlational	Lavin et al. (2003)
	Grey wolf	Coyote	Red fox	0	1	0	Correlational	Sivy et al. (2018)
	Island fox	Island spotted skunk	-	1	0	0	Correlational	Jones et al. (2008)
	Grey wolf	Mountain lion	-	3	0	0	Correlational	Bartnick and Van Deelen (2013), Elbroch et al. (2015), Kortello et al. (2007)

(Continues)

Table 2 Continues

Behaviour	Apex predator	2nd order predator	3rd order predator	Evidence of release			Study design	Citations
				Support	No support	Mixed support		
	Predator community	Eastern fisher	-	0	1	0	Correlational	Lapoint et al. (2015)
	Predator community	Central fisher	-	0	0	1	Correlational	Lapoint et al. (2015)
	Predator community	Pacific fisher	-	0	1	0	Correlational	Lapoint et al. (2015)
	Predator community	Northwest fisher	-	0	1	0	Correlational	Lapoint et al. (2015)
Habitat Use	Predator community	Long-tailed weasel	-	1	0	0	Experimental	St-Pierre et al. (2006)
	Predator community	Long-tailed weasel	Ermine	0	1	0	Experimental	St-Pierre et al. (2006)
	Coyote	Bobcat	-	0	1	0	Correlational	Litvaitis and Harrison (1989)
	Grey wolf	Coyote	-	1	0	1	Experimental	Berger and Gese (2007), Berger et al. (2008)
	Island fox	Island spotted skunk	-	0	0	1	Correlational	Jones et al. (2008)
	Grey wolf	Mountain lion	-	1	0	0	Correlational	Bartnick and Van Deelen (2013)
	Fisher	Grey fox	-	1	0	0	Experimental	Green et al. (2018)
	Fisher	Grey fox	Ringtail	0	1	0	Experimental	Green et al. (2018)

*Support for mesopredator release (MR) hypothesis.

†No support for MR.

#Mixed support for MR.

§Correlational study.

¶Experimental study.

metrics ($n = 9$) similarly found mixed support for release: 44% of studies provided support, 33% provided no support, and 22% provided conflicting support (Table 2).

In contrast to studies investigating changes in distribution and abundance of mesopredators, studies that investigated behavioural changes included a wide variety of apex–mesopredator species pairings ($n = 22$, Table 2). Of these 22 comparisons, 27% ($n = 6$) investigated relationships between two canid species, and 32% ($n = 7$) treated coyotes as an apex or second-order predator. In contrast, 23% ($n = 5$) of comparisons had a felid species as an apex or second-order predator, and 23% ($n = 5$) of comparisons had an ursid species as an apex or second-order predator.

In addition, studies that investigated mesopredator behavioural responses demonstrated high variability among mesopredator species that shared the same apex predator. For example, in a system with mountain lions as an apex predator, bobcats *Lynx rufus*, fishers *Pekania pennanti* and grey foxes *Urocyon cinereoargenteus* reduced their time feeding in areas with mountain lions, whereas coyotes did not alter their feeding behaviours (Allen et al. 2015). In addition, behavioural variability existed among geographically distinct populations of the same mesopredator. For example, Lapoint et al. (2015) observed that fishers in the central part of their range shifted their prey size selection in response to changes in abundance of the apex predator community, whereas fishers in the eastern, Pacific and northwestern populations did not exhibit shifts in diet consistent with MR. Collectively, the variability in behavioural responses of mesopredators to changes in apex predator abundance highlights the complexities of trying to assess behavioural changes as indicators of MR (Fig. 2).

DISCUSSION

A framework for evaluating mesopredator responses

Given the important ecological and conservation implications of MR, clearly defining when and where MR is occurring is critically important. Previous definitions of MR have been vague, variously defining MR as an ‘outbreak’ of mesopredator(s) (Ritchie & Johnson 2009) or as any change in the distribution, abundance or behaviour of a mesopredator in response to apex predator declines (Prugh et al. 2009, Brashares et al. 2010). Based on our review, we believe that a more nuanced definition is needed that accounts for the discernibly different ecological scales at which changes in behaviour (individual), abundance (population) or distribution (species) can occur in response to the apex predator (Fig. 4). Further, these responses are interlinked and deserve careful evaluation of how one

response could scale into impacting another over space and time. For example, changes in individual space use and survival can scale up to population-level collapse or expansion (Brashares et al. 2010), and could ultimately influence distribution of mesopredator species and community assemblies (Newsome et al. 2017). Therefore, we believe that a framework for defining MR needs to be based on the evidence of mesopredator responses across a gradient of spatial, temporal and ecological scales (Fig. 4)

In addition, within a given spatial, temporal or ecological response scale, the relative evidence of a mesopredator response can vary in its weight or ability to support inference. At the finest scale of the individual, indirect spatial overlap measures are weaker evidence of a response than are observed behavioural encounters between apex predators and mesopredators (Fig. 4). For example, an observed aggressive encounter event and subsequent fleeing (Merkle et al. 2009) or mortality (Palomares & Caro 1999) of the mesopredator are more indicative of a mesopredator response to an apex predator than spatial overlap indices (such as home range overlap), given the potential for species to overlap spatially but avoid each other temporally (Wang et al. 2015). Similarly, changes in individual body condition of a mesopredator are weaker evidence of a response than is direct predation by an apex predator. At the population level, shifts over time in the overlap of geographic ranges of apex and mesopredator species provide weaker evidence than documented inverse demographic population trends between apex and mesopredators over time (Fig. 4). While we acknowledge that these ‘stronger’ measures are generally more difficult to investigate in wild mesopredators, our intent is not to discourage the study of the ‘weaker’ measures as a starting point to understand interspecific predator interactions. Rather, given the conflicting evidence for MR observed in our review, our intent is to highlight the relative benefit of certain measures over others, as researchers set objectives and design future field studies.

Defining a threshold for determining mesopredator release

With a framework established for investigating the scales of mesopredator responses, it is possible to define a threshold for when MR could occur more precisely. Fundamentally, the term ‘release’ implies a threshold at which point something, in this case a mid-ranking predator species, has directly benefited. This threshold has been identified in past reviews as being reached when mesopredators expand their distribution, increase their abundance or change their behaviour in response to a decline

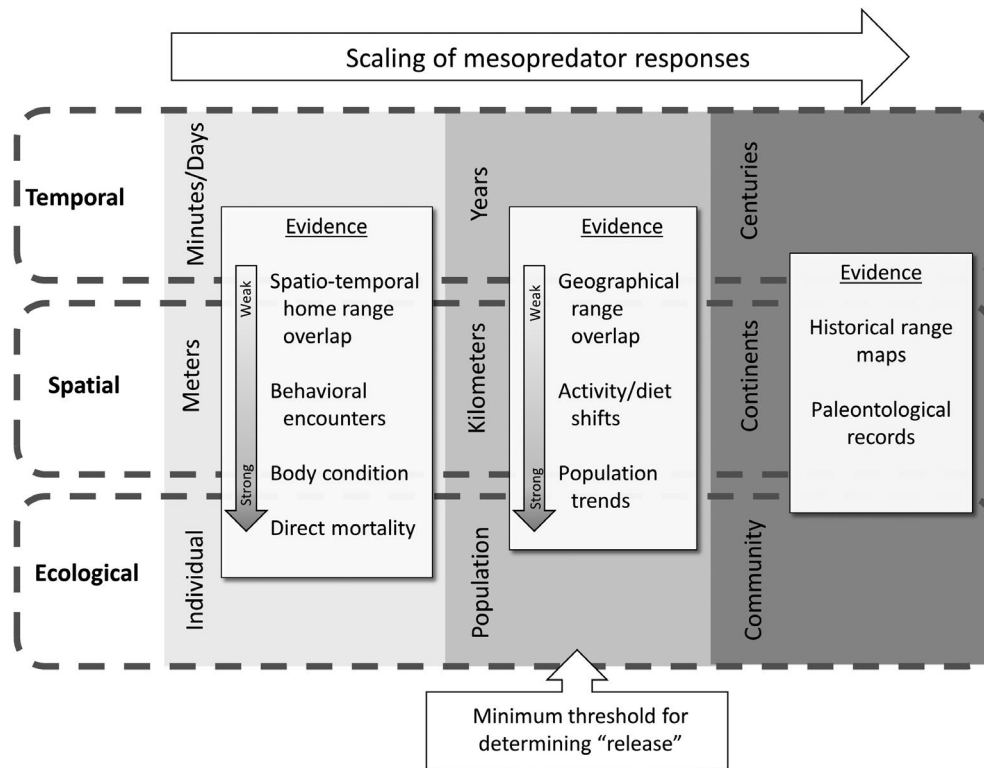


Fig. 4. A proposed framework for evaluating responses of mesopredators to the decline in distribution or abundance of higher-ranking apex predators. Specifically, responses can be observed across a variety of scales temporally, spatially and ecologically (dashed rectangles). Within those scales, evidence can vary in the strength to which it shows a mesopredator response. Within this framework, the threshold for defining when mesopredator release is occurring or has occurred needs to be observed at the population level, over multiple years (middle vertical panel).

in the density or distribution of an apex predator (Prugh et al. 2009, Brashares et al. 2010). Based on our review, it is evident that these thresholds could be achieved at multiple spatial, temporal and ecological scales (Fig. 4). However, we believe that the strongest evidence for MR is achieved when these behavioural, demographic or distributional responses occur over longer periods of time (years rather than hours or days), across greater spatial distances (e.g. kilometres rather than metres), and at the population level rather than the individual level (Fig. 4). Thus, there can be multiple scales of responses by mesopredators to apex predator removal, but in practice we encourage a revised definition of MR that is only applied when loss of apex predators has been documented to drive changes in the abundance of mesopredator populations over a sustained period of time. As in any first attempt to set a definition for an increasingly popular topic in ecology, we expect others to disagree with our threshold and seek to apply MR more widely. Regardless of the subsequent debate and definitions that follow, we challenge authors who suggest that MR is occurring to differentiate short-term changes due to relaxed interspecific competition and MR in their field of study.

Suggestions for improving MR investigations

FOCUSING ON DEMOGRAPHIC RESPONSES

Similar to the current interpretation of risk effects in predator–prey systems being most relevant when changes occur in prey population demography rather than in physiology or behaviour alone (Prugh et al. 2019), we argue that evidence for predator–predator interactions indicative of MR is greatest when there is evidence of a demographic response by the mesopredator. Previous studies have illustrated how the risk of predation influences the behaviour and ultimately the survival of herbivore prey (DeCesare et al. 2014). By contrast, few investigations of interspecific interactions between predators have been able to determine when behavioural responses scale up to demographic responses at the population level. In a study of recolonising grey wolves, Berger et al. (2008) observed increased transient behaviour by coyotes, but no evidence of changes in coyote density. Similarly, following the removal of coyotes, Karki et al. (2007) observed that, despite an increase in swift fox *Vulpes velox* juvenile survival, there was no associated increase in abundance due to increased dispersal

rates by juveniles. Thus, there can be conflicting evidence for MR within individual studies when assessing multiple measures for behaviour, and behavioural changes could reflect complex interactive effects of intra- and inter-specific competition that are not reflected in abundance estimates. Future studies of MR need to be designed to discern the conditions that enable behavioural responses by mesopredators to apex predator loss to scale up to demographic responses at the population level and be indicative of release.

IDENTIFYING APPROPRIATE SPATIAL AND TEMPORAL SCALES FOR ASSESSMENT

Individual studies have provided conflicting evidence for MR when evaluating abundance at different spatial scales. For example, Sivy et al. (2017) found evidence for a negative association between grey wolves and most mesopredator species (supportive of MR) at large spatial scales (i.e. landscape), but a positive association at smaller, local scales (i.e. within a study area). This relationship held for four of the grey wolf—mesopredator species pairings that the authors evaluated, while one species, the American marten *Martes americana*, exhibited the opposite trend. Similarly, Guillaumet et al. (2015) observed limited evidence of a negative association between coyote and lynx *Lynx canadensis* based on historical trapping records at the province scale, but a positive association at the scale of an individual trapline. Thus, care needs to be taken in determining the scale at which it is reasonable to assess MR for each mesopredator species.

In addition to determining the appropriate spatial scale to assess MR, consideration needs to be given to whether an appropriate amount of time has elapsed to detect mesopredator response following apex predator removal. Across all time-series studies ($n = 14$), the average study duration was 15.0 years (SD = 23.5, range = 2–90 years), with no evidence that longer studies (those continuing for more than 10 years) exhibited more consistent trends in support of MR (3 of 7 studies). Functionally, it is likely that in response to the loss of an apex predator, changes in individual mesopredator behaviour will occur first. Behavioural changes may scale up to population-level changes in abundance, which, in turn, could result in changes to mesopredator distribution over time (e.g. Berger & Gese 2007). Thus, behaviour is likely to be the most sensitive metric, where evidence for MR is likely to be detected prior to a change in distribution or abundance. Therefore, even in systems where the loss of an apex predator occurred fairly recently, behavioural responses by mesopredators could provide key early insights into when and where MR is occurring.

EXPERIMENTAL DESIGN

Early in our review of the MR literature, it became apparent that a key difficulty in assessing MR involved the lack of control over apex predator distribution or abundance. Many studies referred to MR without directly observing a change in the distribution or abundance of the apex predator (a key criterion within the existing definition of MR), and were excluded from further review. For example, Lesmeister et al. (2015) and Wang et al. (2015) reported rigorous multi-predator studies across land-use gradients with differing rates of predator occurrence, but these studies were excluded from this review because there were no discrete differences in the distribution or abundance of apex predators. Of the studies included in our review, 19 used spatially distinct areas of differing apex predator density or abundance, 16 used time-series data when apex predators varied in density over time, and two studies considered both spatial and temporal variability. Seven of the studies included the harvest or removal of apex predators as the experimental treatment, but five of these studies (71%) did not support or provide mixed support for MR, raising the question of what intensity of apex predator removal is required before MR is observed. Alternatively, 15 studies used apex predator recolonisation or recovery as the experimental treatment, and eight of these studies (53%) supported MR. However, this requires the assumption that, based on patterns of mesopredator suppression by restored apex predators, in the absence of these apex predators, release would occur. Collectively, while many studies in support of MR were opportunistic in nature, future experiments should be designed such that demographic responses of both apex predators and mesopredators can be monitored pre- and post-impact (i.e. a before-after-control-impact design).

EMBRACING COMPLEXITY

To date, there has been an effort to focus on two-predator systems or two predators within a system, with relatively few attempts to include the responses of multiple predator species simultaneously (Fig. 3). However, with advancements in animal monitoring technology, answers to complex questions are no longer unattainable in multi-predator systems. In addition to traditional Very High Frequency tracking, Global Positioning System-enabled tracking collars have recently been developed that fit even some of the smallest mesopredators (e.g. Harris 2018). The resulting detailed behavioural and survival data could provide a more nuanced understanding of how individual behavioural decisions by a mesopredator in response to an apex predator influence survival and, when replicated across multiple

individuals, these data may provide inference about population-level demographic responses. While capturing, collaring and tracking multiple predator species in a system can be taxing, the use of camera traps (Silver et al. 2004, Jackson et al. 2006) and passive genetic sampling (Gardner et al. 2010) makes it possible to assess changes in abundance of multiple predator species non-invasively and simultaneously.

In addition to technological advancements for monitoring multiple predators in a system, new analytical approaches are being applied to tease apart the contextual factors influencing predator interactions. For example, using multivariate Structural Equation Modelling (SEM; Grace 2008), Sivy et al. (2017) were able to evaluate the relative influence of several environmental covariates, apex predator occupancy and occurrence of all other non-apex predators on occupancy of a given mesopredator species in Alaska. In addition to allowing for the simultaneous assessment of multiple competing hypotheses regarding factors influencing multi-predator interactions (something also accomplished through multi-species occupancy modelling; Rota et al. 2016), SEM can facilitate the inclusion of unobserved (latent) variables such as predation risk and potentially provide an integrated understanding of physiological, behavioural and demographic responses in multi-predator systems (Prugh et al. 2019). Future investigations where measures of predator abundance or relative activity are directly quantified and incorporated in an SEM approach could provide new insights into the multi-scaled dynamics within complex predator communities.

Interpreting support for MR is also continually complicated by the ongoing reshuffling and re-ordering of predator communities in response to human disturbance. In North America, despite having been subject to similar (if not more intensive) human persecution as historical apex predators, coyotes have persisted and expanded across the continent over the past several decades (Flores 2016), taking up the role of apex predator in systems where apex predators have been lost (Gompper 2002). However, there is conflicting evidence on the extent to which coyotes are acting as true apex predators in these systems (Crooks & Soulé 1999, Gehrt & Clark 2003, Fleming et al. 2017). Indeed, in our review, of the 13 studies where coyotes were considered the apex predator, 55% observed support for MR when foxes (grey fox, swift fox, red fox *Vulpes vulpes* or kit fox *Vulpes macrotis*) were the second-order predator, and only 27% were supportive of MR when bobcats were the second-order predator (Fig. 3). In a previous review, Prugh et al. (2009) suggested that coyotes are not historically apex predators in systems and should not be considered a test of MR. However, omitting these studies raises a broader question about the general applicability of MR and lends support to concerns that studies

of MR might be biased towards accumulating evidence to support the conservation of traditional apex predators (Gehrt & Clark 2003, Allen et al. 2011). We suggest that systems dominated by coyotes and other novel apex predators (e.g. dingo, jackal *Canis* spp.) provide a valuable test of MR as a working ecological theory that is testable across systems with different ecological contexts (Fancourt et al. 2019). Further, such information could be vital for creating informed management plans for mesopredator species and for the critical evaluation of the goals and effectiveness of ongoing widescale control or eradication programmes (Gompper 2002, Gehrt & Clark 2003).

CONCLUSIONS

Previous reviews reported MR as occurring frequently throughout North America, to the point of widespread mesopredator 'overabundance' or 'outbreaks' (Prugh et al. 2009, p. 779). In contrast, we found a large amount of conflicting evidence for and against MR, both among and within studies, suggesting that there is a need to re-evaluate how pervasive MR is and to define more clearly when and how the term MR should be applied. Specifically, based on our conceptual framework, we suggest that steps should be taken to advance this field of study, as detailed below.

Firstly, researchers should abandon the widely held assumption that MR is ubiquitous in multi-predator communities that have lost an apex predator, in favour of acknowledging that MR is context-dependent. Evidence for or against MR needs to be weighed based on the spatial, temporal and ecological scales at which the lower-ranking predators' responses are observed. Secondly, we encourage a revised definition of MR that is only applied when the loss of apex predators has been documented to drive changes in the abundance or distribution of mesopredator populations over a sustained period of time. Thirdly, future studies should be designed to assess the conditions under which short-term behavioural responses to relaxed interspecific competition scale up to the population-level processes and species-level distributional changes that are needed to achieve MR. Finally, studies should be conducted to provide a better understanding of how mesopredator diversity (particularly diversity occurring at multiple trophic levels) and global change (e.g. urbanisation and climate change) influence the occurrence of MR, and potential cascading impacts on other trophic levels.

Recognising the complexity of mesopredator responses to apex predator loss and critically examining the validity of MR across systems could have important conservation implications, given the plight of many mammalian predators globally. A quick review of the International Union

for the Conservation of Nature (IUCN) Red List status, trend and threat information for all terrestrial mammalian predator species globally (IUCN 2018) reveals that 70% of apex predator species (as defined by Ripple et al. 2014) are declining, and 10% are increasing. By contrast, for all other non-apex predators, 48% are decreasing while only 3% are increasing globally. Further, for 20% of all non-apex predators globally, there is insufficient information to establish trends or threats, compared to 6% of apex predators (IUCN 2018). Thus, to understand when MR is likely to occur in increasingly reshuffled predator communities with declining apex predators and mesopredators, we suggest that there is a need to shift the focus of MR research away from justifying the recovery of apex predators towards critical evaluations of the ecological mechanisms that govern mesopredator responses.

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