

Research

A simple theory for the mesopredator release effect: when does an apex predator protect their shared prey from a mesopredator?

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Predation plays a variety of important roles in structuring ecological communities. The mesopredator release effect occurs when the removal of an apex predator increases the density of a mesopredator, which in turn reduces the density of their shared prey. The mesopredator release effect can pose significant challenges for predator management and biodiversity conservation. Although several mathematical models have proposed specific circumstances that induce the mesopredator release effect, no theory has yet provided general conditions for this effect. Here, we propose a simple mathematical model to clarify the general conditions that induce the mesopredator release effect. The model predicts that the mesopredator release effect will occur when 1) the carrying capacity of the mesopredator exceeds a certain threshold, and 2) the top-down effect of the apex predator is larger on the mesopredator than on their shared prey. These conditions unify those from previous models and match the existing empirical examples. The simplicity of our theory may be useful for developing system-specific guidelines to control the mesopredator release effect in various ecosystems.

Keywords: apex predator, intraguild predation, invasive species, mathematical model, mesopredator release, shared prey

Introduction

Predation can strongly influence the organization of ecological communities (Aberhan et al. 2006, Terborgh and Estes 2013). Human activities can result in the loss of apex predators and introduce novel predators in extant communities; the resultant alteration of predator fauna may change ecosystem functioning and hamper biodiversity conservation across the globe (Courchamp et al. 2003, Estes et al. 2011). A mesopredator is an intermediate predator that itself is preyed upon by an apex predator. When a native apex predator goes locally extinct or when a non-native apex predator is eradicated, the abundance or foraging activities of some mesopredators may increase, potentially suppressing or extirpating their prey. This cascading-down effect of apex predator loss on the prey of mesopredators is termed the mesopredator release effect. Since the mesopredator release effect predicts that anthropogenic impacts on

predator composition can drive the extinction of prey species, the mesopredator release effect is a significant issue in biodiversity conservation (Crooks and Soulé 1999, Prugh et al. 2009, Ritchie and Johnson 2009).

An influential work of Courchamp et al. (1999) pointed out that the mesopredator release effect could cause an unexpected problem in alien predator management. The problem may arise if conservation practitioners remove a non-native apex predator to protect its native prey from its predation. If the apex predator does not only feed on the native prey but also attack a mesopredator that shares this prey with the apex predator (Fig. 1), the removal of the apex predator can increase the mesopredator, which might subsequently cause an undesirable decrease of the native prey. Currently, the mesopredator release effect is widely recognized as a potential factor that crucially affects the success of invasive predator control (Rayner et al. 2007, Hughes et al. 2019, Peltzer et al. 2019, Preston et al. 2019).

Theoretically, intraguild predation (Holt and Polis 1997) drives the mesopredator release effect. In an intraguild predation module, an intraguild predator and an intraguild prey share common prey species while the intraguild predator also feeds on the intraguild prey. The intraguild predator may correspond to an apex predator, and the intraguild prey to a mesopredator. A mesopredator release effect can occur when a reduction in the intraguild predator density increases the intraguild prey density, which in turn causes a decline in the

density of the shared prey. There is a rich body of theoretical work on the dynamics of intraguild predation (Holt and Polis 1997, Diehl and Feissel 2001, Takimoto et al. 2007, Amarasekare 2008). However, most of these studies focused on the coexistence of an intraguild predator and an intraguild prey (i.e. an apex predator and a mesopredator) without addressing the potential effect on prey species shared by these two predators (i.e. the mesopredator release effect). Although there are some mathematical models of intraguild predation that are focused on the mesopredator release effect (Courchamp et al. 1999, Fan et al. 2005, Russell et al. 2009, Nishijima et al. 2014, Taylor et al. 2016), the theoretical conditions for the mesopredator release effect have remained elusive. For example, although previous models have suggested that alternative prey of a mesopredator could increase the top-down effect of the mesopredator (Fan et al. 2005, Daugherty et al. 2007, Holt and Huxel 2007, Nishijima et al. 2014), it remains unclear when the alternative prey could generate the mesopredator release effect.

It is possible that the theoretical conditions for the mesopredator release effect are not sufficiently understood because mathematical models of intraguild predation can produce complex dynamics. To circumvent this problem, we develop a simple model that can yield well-defined conditions for the mesopredator release effect. To simplify, we treat apex predator density as a controllable parameter (rather than a dynamic variable) by considering that human intervention can control apex predator density. The obtained conditions have intuitive implications that are potentially useful for the management of the mesopredator release effect.

Model

We consider that an apex predator preys on a mesopredator and also a prey of the mesopredator (Fig. 1). The model describes the population dynamics of the shared prey and mesopredator with apex predator density treated as a model parameter:

$$\frac{dP}{dt} = r_p \left(1 - \frac{P}{K_p}\right) P - \alpha_p AP - aMP \quad (1a)$$

$$\frac{dM}{dt} = r_M \left(1 - \frac{M}{K_M}\right) M - \alpha_M AM + baPM \quad (1b)$$

We denote the population density of the shared prey as P , that of the mesopredator as M and that of the apex predator as A . Logistic population growth is assumed for the shared prey and mesopredator. The intrinsic growth rate of the shared prey is r_p , and that of the mesopredator is r_M . The carrying capacity of the shared prey is K_p , and that of the mesopredator is K_M . Linear functional responses are assumed for all trophic interactions involved. The per capita attack rate of the apex predator on the shared prey is α_p , and that on the

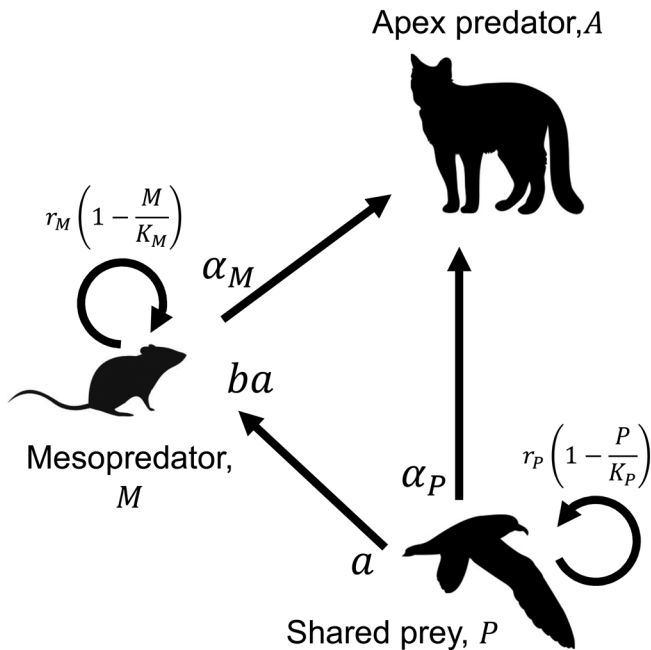


Figure 1. The modeled trophic interactions of the apex predator (A), mesopredator (M) and shared prey (P). The straight arrows represent trophic relationships between a prey species (at arrow tails) and a predator (at arrow heads). The curved arrows for the mesopredator and the shared prey represent their density-dependent population growth in the absence of the trophic interactions depicted by the straight arrows. See Table 1 for definitions of the model parameters. Animal silhouettes are from <www.phylopic.org>.

mesopredator is α_M . The per capita attack rate of the mesopredator on the shared prey is a , and the conversion coefficient of the captured prey into the mesopredator's population growth is b . All parameter values are non-negative. Table 1 summarizes the variables and the parameters of the model.

Analysis

The model is analyzed at equilibrium. The Supporting information provides the details of an analysis of the feasibility and local stability of all equilibria of the model. To determine the conditions for the mesopredator release effect, we focus on the equilibrium at which the shared prey and mesopredator coexist and examine how their equilibrium densities change along the gradient of apex predator density. The details of this analysis are provided in the Supporting information.

Results

Equilibrium densities of the shared prey and mesopredator

The model has four equilibria: extinction equilibrium $(\bar{P}_0, \bar{M}_0) = (0, 0)$, prey-only equilibrium $(\bar{P}_1, 0)$, mesopredator-only equilibrium $(0, \bar{M}_2)$ and coexistence equilibrium (\bar{P}_3, \bar{M}_3) . Table 2 summarizes the equilibrium densities of the shared prey and mesopredator. The model has no alternative stable states (Supporting information).

Conditions for the mesopredator release effect

The mesopredator release effect corresponds to an increase of the mesopredator density and a decline in the shared prey density following a decrease in the density of apex predator. In our model, the mesopredator release effect is thus defined

Table 1. Model variables and parameters. All quantities are non-negative.

Symbol	Definition
Model variable	
M	Mesopredator density
P	Shared prey density
Model parameter	
A	Apex predator density
a	Per capita attack rate of the mesopredator on the shared prey
b	Mesopredator's conversion coefficient of the shared prey
α_M	Per capita attack rate of the apex predator on the mesopredator
α_P	Per capita attack rate of the apex predator on the shared prey
r_M	Mesopredator's intrinsic growth rate
r_P	Shared prey's intrinsic growth rate
K_M	Mesopredator's carrying capacity
K_P	Shared prey's carrying capacity

as the mesopredator density being a decreasing function of the apex predator density ($\partial \bar{M}_3 / \partial A < 0$) while the shared prey density is an increasing function of the apex predator density ($\partial \bar{P}_3 / \partial A > 0$). Because the apex predator density always reduces the mesopredator density ($\partial \bar{M}_3 / \partial A < 0$, see the expression in Table 2), the condition for the apex predator to increase the shared prey density ($\partial \bar{P}_3 / \partial A > 0$) defines the mesopredator release effect. This condition can be formulated as:

$$K_M > \frac{\alpha_P}{a} \times \frac{r_M}{\alpha_M} \quad (2)$$

This condition states that the carrying capacity of the mesopredator (K_M) should exceed a certain threshold ($\alpha_P r_M / a \alpha_M$). However, this condition is not sufficient for inducing the mesopredator release effect; additional conditions to guarantee a feasible coexistence equilibrium are necessary. The coexistence equilibrium is feasible when either of the following conditions is satisfied (Supporting information).

$$K_M < \frac{r_P}{a} \quad (3)$$

or

$$\frac{\alpha_M}{r_M} > \frac{\alpha_P}{r_P} \quad (4)$$

As illustrated in Fig. 2, condition 2 together with condition 3 or 4 is necessary and sufficient for the mesopredator release effect to be possible. Condition 3 states that the carrying capacity of the mesopredator (K_M) should not be too large. When this condition holds, the shared prey can coexist with the mesopredator in the absence of the apex predator (the regions for patterns I–III in Fig. 2, more details provided in the next section). Otherwise, the shared prey cannot coexist with the mesopredator without the apex predator because the predation of the mesopredator on the shared prey is too strong. Nonetheless, their coexistence is possible when the apex predator is sufficiently abundant if condition 4 holds (the region for pattern IV in Fig. 2, more details provided in the next section). Condition 4 means that the predation effect of the apex predator on the mesopredator's population growth (α_M / r_M) is larger than that on the population growth of the shared prey (α_P / r_P).

Condition 4 is satisfied when conditions 2 and 3 are simultaneously satisfied (i.e. the region where condition 4 holds contains the region where both 2 and 3 hold in Fig. 2, Supporting information). As a result, conditions 2 and 4 are necessary and sufficient for the mesopredator release effect to be observed (over a given range of apex predator densities). This condition assumes a positive intrinsic growth rate of a mesopredator ($r_M > 0$) but is robust to considering a negative intrinsic growth rate (Supporting information).

Table 2. Equilibrium densities of the shared prey and mesopredator.

Equilibrium	Shared prey	Mesopredator
Extinction	$\bar{P}_0 = 0$	$\bar{M}_0 = 0$
Prey only	$\bar{P}_1 = K_P \left(1 - \frac{\alpha_P}{r_P} A\right)$	$\bar{M}_1 = 0$
Mesopredator only	$\bar{P}_2 = 0$	$\bar{M}_2 = K_M \left(1 - \frac{\alpha_M}{r_M} A\right)$
Coexistence	$\bar{P}_3 = \frac{K_P [r_P r_M - a r_M K_M + (a \alpha_M K_M - \alpha_P r_M) A]}{b a^2 K_P K_M + r_P r_M}$	$\bar{M}_3 = \frac{K_M [r_P r_M + b a r_P K_P - (b a \alpha_P K_P + \alpha_M r_P) A]}{b a^2 K_P K_M + r_P r_M}$

Range of apex predator densities leading to the mesopredator release effect

The range of apex predator densities at which the mesopredator release effect is observed depends on conditions 3 and 4 for a feasible coexistence equilibrium. When the coexistence equilibrium is feasible, the responses of shared prey and mesopredator densities along the gradient of apex predator densities show four distinct patterns I–IV (Fig. 3, defining conditions and characteristics of patterns I–IV are derived in the Supporting information and summarized in the Supporting information). The mesopredator release effect is observed in patterns I and IV, while the effect does not occur in patterns II and III.

In all patterns, mesopredator densities are positive in the absence of the apex predator ($A=0$) and decrease as the apex predator becomes more abundant. Pattern I–III are all characterized by a positive shared prey density in the absence of the apex predator. In pattern I, the shared prey density (\bar{P}_3) increases as the apex predator becomes more abundant (i.e. the

mesopredator release effect), until the apex predator density reaches a critical value ($A = A_{M3}^*$) at which the mesopredator is driven extinct ($\bar{M}_3 = 0$ and $\bar{P}_3 = \bar{P}_1$) (Fig. 3a). Further increases in apex predator densities decrease the shared prey to extinction ($\bar{P}_1 = 0$ when $A = A_{P1}^*$). In pattern II and III, the shared prey (\bar{P}_3) and the mesopredator (\bar{M}_3) decreases monotonically with increasing densities of the apex predator (A) (no mesopredator release effect, Fig. 3b, c). In pattern II, this increase in the apex predator causes the extinction of the mesopredator first ($\bar{M}_3 = 0$ and $\bar{P}_3 = \bar{P}_1$ at $A = A_{M3}^*$), and then the extinction of the shared prey ($\bar{P}_1 = 0$ at $A = A_{P1}^*$) (Fig. 3b). By contrast, in pattern III, the increase of apex predator densities firstly drives the shared prey into extinction ($\bar{P}_3 = 0$ and $\bar{M}_3 = \bar{M}_2$ at $A = A_{P3}^*$) and then exterminates the mesopredator ($\bar{M}_2 = 0$ at $A = A_{M2}^*$) (Fig. 3c). In pattern IV, the shared prey cannot coexist with the mesopredator in the absence of the apex predator ($A=0$) but can persist with the mesopredator at some intermediate densities of the apex predator ($A_{P3} < A < A_{M3}^*$) and increases with increasing apex predator densities (the mesopredator release effect, Fig. 3d). The mesopredator is driven extinct at the upper limit of this range ($\bar{M}_3 = 0$ and $\bar{P}_3 = \bar{P}_1$ at $A = A_{M3}^*$), and a shared prey extinction follows at a higher apex predator density ($\bar{P}_1 = 0$ when $A = A_{P1}^*$).

Discussion

The mesopredator release effect can cause a problem that population reduction in an apex predator results in an unexpected decline of its prey, if the apex predator not only attacks the prey but also a mesopredator sharing the prey with the apex predator (Courchamp et al. 1999). Although the mesopredator release effect can be widely important for biodiversity conservation and ecosystem management, the theoretical conditions for the mesopredator release effect have remained underdeveloped. In this study, we developed a simple mathematical model and identified two simple conditions for the mesopredator release effect. First, the carrying capacity of the mesopredator must exceed a certain threshold; $K_M > \alpha_P r_M / a \alpha_M$. Second, the top-down effect of the apex predator must be stronger on the mesopredator than on the shared prey; $\alpha_M / r_M > \alpha_P / r_P$.

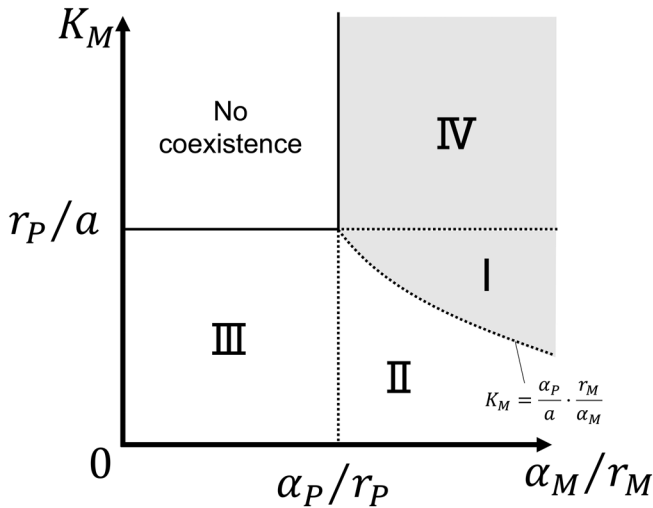


Figure 2. The conditions for the mesopredator release effect. The mesopredator release effect is expected in the shaded regions. The four response patterns I–IV of shared prey and mesopredator densities to apex predator densities are expected in respective parameter regions.

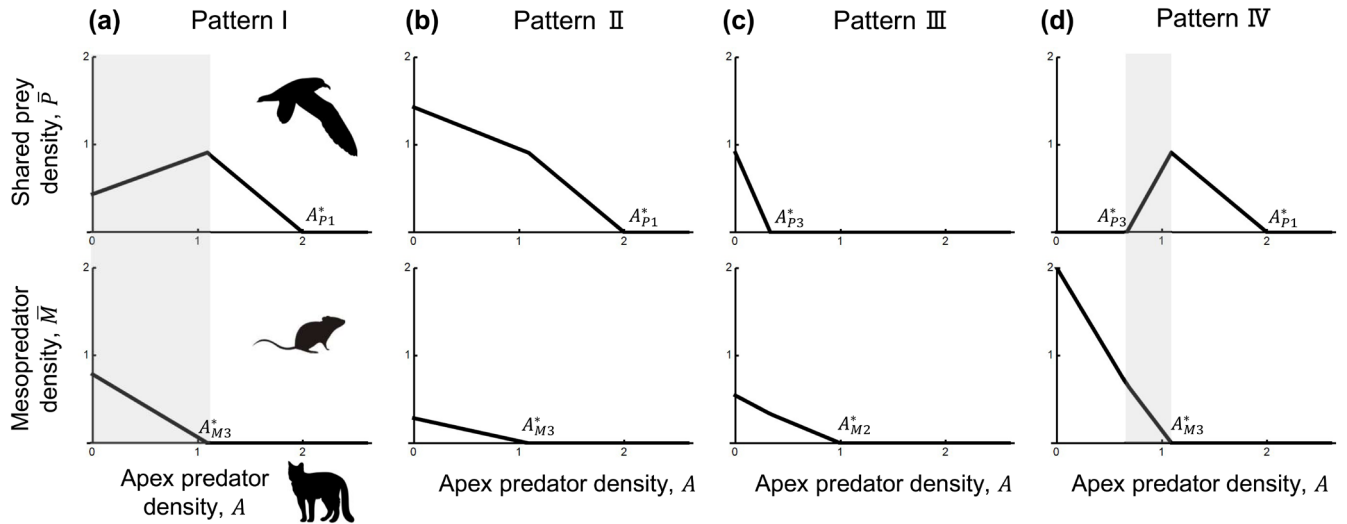


Figure 3. Four patterns of the responses of shared prey and mesopredator densities to apex predator densities when the shared prey and mesopredator can coexist. (a) pattern I, (b) pattern II, (c) pattern III and (d) pattern IV. The mesopredator release effect is observed in patterns I and IV across the shaded ranges of apex predator densities. Parameter values changed are $K_M=0.75$ and $\alpha_p=0.5$ in (a), $K_M=0.25$ and $\alpha_p=0.5$ in (b), $K_M=0.5$ and $\alpha_p=2$ in (c) and $K_M=2$ and $\alpha_p=0.5$ in (d). Other fixed parameters are $a=1$, $b=0.1$, $\alpha_M=1$, $r_M=1$, $r_p=1$ and $K_p=2$. The threshold apex predator densities are derived in the Supporting information: $A_{P1}^* = \frac{r_p}{\alpha_p}$ (Eq. S9), $A_{P3}^* = \frac{ar_M K_M - r_p r_M}{a\alpha_M K_M - \alpha_p r_M}$ (Eq. S12), $A_{M2}^* = \frac{r_M}{\alpha_M}$ (Eq. S15) and $A_{M3}^* = \frac{bar_p K_p + r_p r_M}{ba\alpha_p K_p + \alpha_M r_p}$ (Eq. S7). Animal silhouettes are from <www.PhyloPic.org>.

The first condition is informative. The mesopredator release effect requires that a mesopredator mediating the effect has a carrying capacity larger than a certain threshold. This condition suggests that interactions between top-down and bottom-up effects on the mesopredator is important for the mesopredator release effect. That is, even when a reduction in apex predator densities lessens the top-down control over the mesopredator population, a sufficiently large carrying capacity is necessary for generating a bottom-up effect of increasing the mesopredator density so as to intensify the mesopredator's predation on the shared prey. An empirical example agrees with this interpretation. In southern Sweden, bottom-up effects from favorable bioclimatic conditions increased mesopredators (the red fox, *Vulpes vulpes*) after the reduction of apex predators (wolves, *Canis lupus*, and Eurasian lynx, *Lynx lynx*) (Elmhagen and Rushton 2007), and predation by the increased red fox affected black grouse *Lyrurus tetrix*, mountain hare *Lepus timidus* and ptarmigan *Lagopus* spp. (Elmhagen and Rushton 2007, Breisjøberget et al. 2018, Henden et al. 2021). In contrast, in the northern parts, no mesopredator effect was observed likely because less favorable climatic conditions were responsible for a lower carrying capacity for the red fox.

Alternative prey to mesopredators (i.e. supplementary prey items utilized by a mesopredator in addition to the focal shared prey) can be a significant bottom-up factor that can affect the carrying capacity of mesopredators (K_M). Our first condition that a larger carrying capacity of mesopredators will promote the mesopredator release effect is parallel to the previous theoretical finding that alternative prey promotes

the mesopredator release effect (Nishijima et al. 2014). Many cases of mesopredator release effects seem to have been driven by alternative prey to mesopredators (Taylor et al. 2016; reviewed by Nishijima et al. 2014). However, alternative prey might also increase the intrinsic growth rate of mesopredators (r_M). A larger intrinsic growth rate makes stringent our first and second conditions. Thus, if alternative prey increases the intrinsic growth rate without affecting the carrying capacity, alternative prey might rather prevent the mesopredator release effect. Moreover, our first condition illustrates another potential role of alternative prey in determining the mesopredator release effect. Higher densities of alternative prey can decrease the attack rate of the mesopredator on the shared prey if alternative prey causes mesopredator's prey switching from the shared prey (a switching functional response) or takes up the limited foraging time of the mesopredator (a saturating functional response). Decreasing the mesopredator's attack rate on the shared prey (a) increases the threshold ($\alpha_p r_M / \alpha_M$) above which the mesopredator's carrying capacity drives the mesopredator release effect. Thus, if higher densities of alternative prey both increase the carrying capacity and decrease the attack rate on the shared prey, alternative prey can either promote or prevent the mesopredator release effect. This preventive effect of alternative prey might explain some empirical examples in which the expected mesopredator release effect was not observed. For example, on an island in New Zealand, eradication of an introduced apex predator (the feral cat *Felis catus*) induced a mesopredator release effect of the Pacific rat *Rattus exulans* on the breeding success of Cook's petrel *Pterodroma cookii*

at high altitude sites but not at low altitude sites, although alternative food for the Pacific rat seemed more abundant at low altitude sites (Rayner et al. 2007). If abundant alternative food shifts the foraging effort of the Pacific rat away from Cook's petrel, however, it decreases the attack rate (a) and thus elevates the threshold, which tightens the first condition for the mesopredator release effect. Overall, our first and second conditions suggest multiple potential mechanisms by which alternative prey to mesopredators may promote or hinder the mesopredator release effect.

Other ecological factors, such as intra- and interspecific competition and disease, might also limit the carrying capacity of a mesopredator, affecting our first condition. Impacts of competition and disease might be strong when the mesopredator reaches high densities after being released from a top-down control by an apex predator. High densities might intensify intraspecific competition in a mesopredator (e.g. territorial conflicts in coyotes; Morin and Kelly 2017) and interspecific competition among mesopredators (e.g. potential interspecific competition from goshawks *Accipiter gentilis* on buzzards *Buteo buteo* in the absence of eagle owls *Bubo bubo*; Chakarov and Krüger 2010). Disease might also strongly regulate a mesopredator population (e.g. sarcoptic mange in red foxes and coyotes *Canis latrans*; Lindström et al. 1994, Chronert et al. 2007), potentially limiting its carrying capacity. These antagonistic interactions that negatively affect mesopredators may lower the likelihood of the mesopredator release effect.

The second condition for the mesopredator release effect states that the top-down effect of the apex predator must be stronger on the mesopredator (α_M/r_M) than that on the shared prey (α_P/r_P). When this condition holds, increasing the apex predator density causes the extinction of the mesopredator before the shared prey goes extinct (pattern I, II and IV). This means that the shared prey can tolerate higher apex predator densities than the mesopredator does; that is, the shared prey is superior to the mesopredator in apparent competition mediated by the apex predator. Thus, this condition implies that the mesopredator release effect and the hyperpredation effect (i.e. a negative impact via apparent competition by the mesopredator on the shared prey in this case; Courchamp et al. 2000) are theoretically mutually exclusive, in agreement with empirical examples (Ringler et al. 2015). Notably, although this condition might appear to suggest that increasing apex predators could be used as a potential strategy for eradicating non-native mesopredators, it would also decrease native prey and put them at risk of extinction.

To derive concise conditions for the mesopredator release effect, our model compromises detailed characteristics of real systems in several respects. First, the model assumes that the apex predator density is a parameter controlled by extrinsic factors. This simplification not only powerfully facilitates the model analysis but is also valid in many practical cases in which, for example, human intervention can control non-native apex predators. However, this simplification excludes dynamic responses of an apex predator population to human intervention and changes in the densities

of mesopredators and shared prey. For example, while overcompensation of invasive predator populations might drive unexpected increases in their densities after they are removed (Grosholz et al. 2021), our model does not consider such overcompensation. Second, our model assumes that predators exhibit linear functional responses to their prey densities. Linear functional responses, together with a constant apex predator density, might have precluded complex community dynamics, such as alternative stable states and non-equilibrium coexistence, which were found in more complex models of intraguild predation (Holt and Polis 1997, Tanabe and Namba 2005, Takimoto et al. 2007, Nishijima et al. 2014). More complex models tailored with these features may be useful for yielding predictions that are specifically applicable to particular systems (Taylor et al. 2016). Third, our simple model deals only with the three focal species of apex predators, mesopredators and their shared prey. This approach may be relevant when the focal species interact strongly in isolation, as we might expect for an island system with few other interacting species. However, it can overestimate the possibility of mesopredator release effects if the focal system is embedded in a complex community, in which case the top-down effects of focal predators might be weakened (Lloyd 2007). Fourth, our model does not incorporate any changes in prey behavior induced by predators. Fear-mediated behavioral modifications may be widespread among mesopredators and their prey shared with apex predators, potentially altering the mesopredator release effect (Berger 2010). Developing a theory that integrates such fear effects can yield more practical and useful guidelines for managing mesopredator release effects (Gaynor et al. 2021). Finally, our model assumes that a mesopredator can persist without shared prey unless apex predators are too abundant. However, a mesopredator might not subsist without shared prey; for example, if a mesopredator is a specialist predator that only feeds on the shared prey, the mesopredator might not survive without the shared prey even in the absence of apex predators. Our additional analysis suggests that the mesopredator release effect in such a case requires that density-dependent regulation of a mesopredator population must be sufficiently weak (Supporting information), which is essentially analogous to our first condition on the carrying capacity of the mesopredator.

The mesopredator release effect can complicate ecosystem restoration involving apex predator reintroductions or non-native apex predator management (Zavaleta et al. 2001, Lavers et al. 2010, Ritchie et al. 2012). Difficulty in evaluating the potential of mesopredator release effects arises because multiple biotic and abiotic factors can affect the ecological impacts of apex predators in a complex manner (Zavaleta et al. 2001, Allen et al. 2013). Our conditions for the mesopredator release effect succinctly summarize the effects of such complex interactions of multiple factors. Evaluating the parameters involved in these conditions could allow us to estimate the likelihood of a mesopredator release effect for specific target systems. For example, diet analysis of apex predators and mesopredators may be

used to inform their top-down effects on their shared prey (Wysong et al. 2019); the diet information of a mesopredator can also be used to assess its carrying capacity if productivities of the diet items are available. These pieces of information could be integrated into the conditions that we provide here to forecast the possibility of the mesopredator release effect. The simplicity of our theory may be useful in developing guidelines for controlling the mesopredator release effect.

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Author contributions

Gaku Takimoto: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Shota Nishijima:** Conceptualization (supporting); Validation (equal); Writing – review and editing (equal).

Data availability statement

Data are available at Zenodo Digital Repository <<https://doi.org/10.5281/zenodo.6379088>> (Takimoto and Nishijima 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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